

# FINAL REPORT

Using a Hierarchical Approach to Model Regional Source-Sink  
Dynamics for Neotropical-Nearctic Songbirds to Inform  
Management Practices on Department of Defense Installations

SERDP Project RC-2121

MARCH 2017

Dr. Peter P. Marra  
Thomas B. Ryder  
Scott Sillett  
**Smithsonian Institution**

Matthew Betts  
**Oregon State University**

Rodney Siegel  
Jim Saracco  
**Institute for Bird Populations**

Rich Fischer  
**US Army Research and Development Center**

*Distribution Statement A*

*This document has been cleared for public release*



*Page Intentionally Left Blank*

This report was prepared under contract to the Department of Defense Strategic Environmental Research and Development Program (SERDP). The publication of this report does not indicate endorsement by the Department of Defense, nor should the contents be construed as reflecting the official policy or position of the Department of Defense. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the Department of Defense.

*Page Intentionally Left Blank*

REPORT DOCUMENTATION PAGE			Form Approved OMB No. 0704-0188	
Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing this collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden to Department of Defense, Washington Headquarters Services, Directorate for Information Operations and Reports (0704-0188), 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to any penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number. <b>PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.</b>				
1. REPORT DATE (DD-MM-YYYY) 03-20-2017		2. REPORT TYPE Final Report		3. DATES COVERED (From - To) 2/3/11-6/30/17
4. TITLE AND SUBTITLE  Using a Hierarchical Approach to Model Regional Source-Sink Dynamics for Neotropical-Nearctic Songbirds to Inform Management Practices on Department of Defense Installations.			5a. CONTRACT NUMBER	
			5b. GRANT NUMBER	
			5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S) Mara, Peter P. Ryder, Thomas B. Sillett, Scott Betts, Matthew Siegel, Rodney; Saracco, Jim; Fischer, Rich			5d. PROJECT NUMBER	
			5e. TASK NUMBER	
			5f. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES)  Smithsonian Migratory Bird Center 3001 Connecticut Avenue NW Washington, DC 20008			8. PERFORMING ORGANIZATION REPORT NUMBER	
9. SPONSORING / MONITORING AGENCY NAME(S) AND ADDRESS(ES) Strategic Environmental Research and Development Program 4800 Mark Center Drive, Suite 17D03 Alexandria, VA 22350			10. SPONSOR/MONITOR'S ACRONYM(S)  SERDP	
			11. SPONSOR/MONITOR'S REPORT NUMBER(S)  RC-2121	
12. DISTRIBUTION / AVAILABILITY STATEMENT  Unlimited				
13. SUPPLEMENTARY NOTES				
14. ABSTRACT The decline of Nearctic-Neotropical migratory birds over the last two-decades remains one of the most pressing issues in conservation biology. The DoD manages 25 million acres of land and has the joint responsibility of managing these high-quality forest, desert, prairie, and other lands while concurrently engaging in military readiness activities that can alter the structure and function of those habitats. Given that forest loss and fragmentation threaten terrestrial biodiversity worldwide, it is critical for DoD to understand what species are affected by these processes. Among vertebrate taxa, the DoD has taken an active role in the conservation and management of Neotropical-Nearctic migratory birds. DoD properties serve as critical habitat for several avian species of concern with many installations having been designated as Important Bird Areas. For continued effective management of migratory bird populations on DoD installation, both the spatial and temporal changes in distribution and dynamics of avian populations must be actively monitored.				
15. SUBJECT TERMS <i>Dynamic Occupancy, Hylocichla mustelina, Intensive Demography, Monitoring Avian Productivity and Survivorship, Point-counts, Population Growth, Source-sink Dynamics, Species of Concern, Wood thrush</i>				
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT  U	18. NUMBER OF PAGES  106
a. REPORT UU	b. ABSTRACT UU	c. THIS PAGE UU		
				19b. TELEPHONE NUMBER (include area code) 202-633-1594

*Page Intentionally Left Blank*

## Table of Contents

<b>Executive Summary .....</b>	<b>Pg. 1</b>
<b>Smithsonian Institution-Thomas B. Ryder &amp; Peter P. Marra</b>	
 <b>Chapter 1 .....</b>	 <b>Pg. 4</b>
<b>Using dynamic occupancy and species distribution models to understand species sensitivity to landscape configuration</b>	
<b>Oregon State University- Jonathon J. Valente &amp; Matt Betts</b>	
 <b>Chapter 2 .....</b>	 <b>Pg. 56</b>
<b>Estimating vital rates of Wood thrush at Monitoring Avian Productivity and Survivorship (MAPS) Stations</b>	
<b>Institute for Bird Populations- James F. Saracco &amp; Danielle R. Kaschube</b>	
 <b>Chapter 3 .....</b>	 <b>Pg. 68</b>
<b>Demography across the annual cycle: spatial and temporal variation in vital rates drives population dynamics in Wood thrush</b>	
<b>Smithsonian Institution- Clark Rushing, Scott Sillett, Peter Marra &amp; Thomas B. Ryder</b>	
 <b>Chapter 4 .....</b>	 <b>Pg. 86</b>
<b>Synthesizing what different methodological approaches tell us about avian demography on Department of Defense installations</b>	
<b>Smithsonian Institution &amp; Oregon State - Thomas B. Ryder &amp; Jonathon Valente</b>	

## List of Tables

<b>Table 1.1</b>	Distribution of forest patch and demographic plot point count stations	Pg. 9
<b>Table 1.2</b>	Raw counts and naïve occupancy estimates for all species	Pg. 21-22
<b>Table 1.3</b>	Summary of vegetation local and landscape level habitat features	Pg. 23
<b>Table 1.4</b>	Results of the principal components analysis for local vegetation	Pg. 23
<b>Table 1.5</b>	Results from occupancy models fit to simulated datasets	Pg. 27
<b>Table 1.6</b>	Results from abundance models fit to simulated datasets	Pg. 28
<b>Table 1.7</b>	Results from occupancy models fit to simulated datasets	Pg. 29
<b>Table 1.8</b>	Results from abundance models fit to simulated datasets	Pg. 30
<b>Table 1.9</b>	The 19 species for which site closure was evaluated	Pg. 31
<b>Table 1.10</b>	Estimates, errors, and tests for effects of covariates on occupancy	Pg. 36
<b>Table 1.11</b>	Estimates, errors, and tests for effects of covariates on colonization	Pg. 37
<b>Table 1.12</b>	Estimates, errors, and tests for effects of covariates on extinction	Pg. 38
<b>Table 1.13</b>	Covariate effects on occupancy probabilities for 52 bird species	Pg. 40
<b>Table 1.14</b>	Area under the curve for boosted regression trees models	Pg. 46
 <b>Table 2.1</b>	 MAPS stations operated in southern Indiana 2011-214	 Pg. 57-58
<b>Table 2.2</b>	Annual effort (net-hours) completed at the 18 MAPS stations	Pg. 58
<b>Table 2.3</b>	Summary of year-unique captures for (MAPS) stations	Pg. 61-63
 <b>Table 3.1</b>	 Vital rate estimates and contributions to variation in population growth	 Pg. 74
 <b>Table 4.1</b>	 Population growth estimates for diverse avian sampling techniques	 Pg. 91-92
<b>Table 4.2</b>	Models to test the effects of variables on self-recruitment rate	Pg. 95



## List of Figures

<b>Figure 1.1</b>	The processes that can lead to closure violations for mobile animals	Pg. 8
<b>Figure 1.2</b>	Locations of all point count surveys from 2011-2014	Pg. 10
<b>Figure 1.3</b>	A schematic outlining the structure of the occupancy and abundance datasets	Pg. 14
<b>Figure 1.4</b>	TM band 1 data from the aerial Landsat 5 image	Pg. 20
<b>Figure 1.5</b>	A comparison of open occupancy and abundance estimates	Pg. 32
<b>Figure 1.6</b>	A comparison of open occupancy and abundance estimates	Pg. 33
<b>Figure 1.7</b>	Sampling time frame for estimating population dynamics from count data	Pg. 34
<b>Figure 1.8</b>	Correlation coefficients between occupancy, colonization and extinction	Pg. 35
<b>Figure 1.9</b>	Effects of landscape variables on community distribution patterns	Pg. 42
<b>Figure 1.10</b>	Effects of landscape variables on community richness patterns	Pg. 43
<b>Figure 1.11</b>	Conservation concern scores for bird community groups	Pg. 45
<b>Figure 1.12</b>	The relative influence of covariates on species distributions by scale	Pg. 47
<b>Figure 1.13</b>	The relative influence of covariates on species distributions by data source	Pg. 47
<b>Figure 1.14</b>	Wood thrush species distribution model (SDM)	Pg. 48
<b>Figure 2.1</b>	Reproductive index for age-specific capture data from 18 MAPS stations	Pg. 63
<b>Figure 2.2</b>	MAPS reproductive index across the range of 2-km forest cover values	Pg. 64
<b>Figure 2.3</b>	Adult apparent survival rate estimates derived from 18 MAPS stations	Pg. 64
<b>Figure 2.4</b>	Correlation between MAPS and demographic monitoring survival estimates	Pg. 65
<b>Figure 3.1</b>	Map of linked populations of Wood Thrush used for IPM	Pg. 70
<b>Figure 3.2</b>	Contribution of breeding season vital rates to population growth	Pg. 75
<b>Figure 3.3</b>	Contributions of annual vital rates to population growth	Pg. 76
<b>Figure 3.4</b>	Contribution of vital rates across a habitat quality gradient population growth	Pg. 77
<b>Figure 4.1</b>	A comparison of population growth estimates from different methods	Pg. 92
<b>Figure 4.2</b>	Large trees predict Wood thrush demographic performance	Pg. 93
<b>Figure 4.3</b>	Predicted Wood Thrush occupancy as a function of number of large trees	Pg. 94

## List of Acronyms

AIC- Akaike information criterion  
AUC- Area under the curve  
BONWR- Big Oaks National Wildlife Refuge  
BRT- Boosted regression tree  
CJS- Cormack Jolly Seber  
CRANE- Naval Support Activity Crane  
DoD- Department of Defense  
GLM- Generalized linear model  
HDPI- Highest posterior density interval  
IBP- Institute for Bird Populations  
IDNR- Indiana Department of Natural Resources  
IPM- Integrated population model  
LTRE- Life table response experiments  
MCMC- Monte Carlo Markov chain  
OSU- Oregon State University  
PC- Principle component  
RI- Reproductive index  
SDM- Species distribution models  
SMBC- Smithsonian Migratory Bird Center  
TE- Temporary emigration  
USGS- US Geological Survey

## Keywords

*Dynamic Occupancy, Hylocichla mustelina, Intensive Demography, Monitoring Avian Productivity and Survivorship, Point-counts, Population Growth, Source-sink Dynamics, Species of Concern, Wood thrush*

**Acknowledgements-Oregon State University**

We are sincerely grateful to Kelsey McCune, Anna Tucker, Brian Slaby, Gordon Gover, Shawn Duncan, Carl Bochmann, Christina Slover, Christa LeGrande, Abigail Burns, Joshua Suich, Christopher Winter, Marcel Villar, Vincent Johnson, Samantha Wolfe, Rachel Gardner, Robert Snowden, Lauren Gillespie, Ryan Ubias, and Ellen Comeau for their tireless field efforts that made this project such a success. We also thank the wonderful people on all of the state parks, wildlife refuges, national forests, nature preserves and private properties who helped to manage the logistics of this effort. In particular, we thank all of the personnel at West Boggs Park in Loogootee, Indiana for housing our field crews and going above and beyond to make us feel like a welcome part of their community.

**Acknowledgements-Institute for Bird Populations**

We are grateful to all our field biologist interns (Todd Alleger, Matt Bristol, Mary Chapman, Jessica Gonzalez, Samantha Goss, Marcy Harsaran, Katherine Jackson, Emily BONWRreys, Victor Koos, Aileen Lennon, Melanie Mancuso, Libby Megna, Kevin Mortinson, Alison Nevins, Ben Nickley, Michael Novak, Meghan Oberkircher, Luke Oliver, Catherine Pham, Kaitlin Pizzi, Catie Porro, Emily Prosser, Sara 'Ruby' Rozell, Erica Skorlinski, Claire Woolf, and Danica Zupic) and field biologists (Mike Arnold, James Junda, and Keegan Tranquillo). We would also like to thank the personnel at Big Oaks National Wildlife Refuge, Hoosier National Forest, Martin State Forest, McCormick Creek State Park, Naval Surface Warfare Center Crane, Owen-Putnam State Forest, and Spring Mill State Park for their support of this program and the banding on their lands. This is Contribution Number 540 of The Institute for Bird Populations.

**Acknowledgements- Smithsonian Institution**

Thanks to the 72 field biologists who helped collect demographic data across the four time frame of the study. Clark Rushing was also supported by the George Didden Conservation fund at the National Zoological Park. The authors thank T. Will, C. Stanley, V. Ruiz-Gutierrez, J. Hall, J. Valente, J. Robb, S. Andrews, L. Petercheff, R. Hedge, S. Haulton, & M. Mycroft for assistance with funding, data collection, and model development.

## Executive Summary

The decline of Nearctic-Neotropical migratory birds over the last two-decades remains one of the most pressing issues in conservation biology. The DoD manages 25 million acres of land and has the joint responsibility of managing these high-quality forest, desert, prairie, and other lands while concurrently engaging in military readiness activities that can alter the structure and function of those habitats. Given that forest loss and fragmentation threaten terrestrial biodiversity worldwide, it is critical for DoD to understand what species are affected by these processes. Among vertebrate taxa, the DoD has taken an active role in the conservation and management of Neotropical-Nearctic migratory birds. DoD properties serve as critical habitat for several avian species of concern with many installations having been designated as Important Bird Areas. For continued effective management of migratory bird populations on DoD installation, both the spatial and temporal changes in distribution and dynamics of avian populations must be actively monitored.

Characterizing how populations are spatially structured by demographic processes across heterogeneous habitats (source-sink dynamics) remains an important monitoring tool. High quality, source habitats typically yield a demographic surplus where births exceed deaths, and emigration exceeds immigration, whereas low quality, sink habitats generate demographic deficits where deaths exceed births and immigration exceeds emigration. To date, a variety of approaches that vary greatly in effort and data resolution have been used to determine population growth trajectories and persistence probabilities. This hierarchy of methodological approaches includes: 1) point-counts that provide coarse demographic data on distribution, abundance, and richness and can be implemented over large spatial-scales with low unit effort, 2) Monitoring Avian Productivity and Survivorship that provide higher resolution demographic data on some vital rates (e.g., survival), but are limited in scale largely because of unit effort and, 3) intensive demographic monitoring that can provide high resolution demographic data on most vital rates, but is also limited in spatial monitoring extent and requires the greatest unit effort.

In order to implement cost-effective management of avian populations, DoD land managers need comparative information about the efficacy of different avian monitoring protocols and the spatial scale at which they can characterize population dynamics. Avian point-counts and occupancy modeling have become a widespread tool used to indirectly categorize sources and sink habitats and while these tools have been shown to be effective for detecting population change at a regional scale, less is known about their reliability for quantifying local population dynamics. The DoD has used the Monitoring Avian Productivity and Survivorship (MAPS) monitoring protocols on their installations to generate indices of fecundity, estimates of density, and apparent survival, but the ability of this approach to accurately quantify source-sink dynamics at a scale relevant for management have yet to be tested. In contrast to point-counts and MAPS, intensive demographic monitoring has long been the gold standard for estimating population growth ( $\lambda$ ), but this approach is both labor intensive and can be cost prohibitive. Although intensive demographic approaches have been widely used to estimate lambda, the majority of these models have focused solely on breeding season vital rates, despite growing evidence about the importance of non-breeding season demography on population dynamics. To date, no studies have compared how these hierarchical approaches perform for characterizing source-sink dynamics and to identify the factors that drive population persistence.

A second element of effective management is the ability to link demographic vital rates and the subsequent growth of populations to both local habitat quality and landscape configuration. Past work on DoD installations in the Midwest, indicate that forest amount is often a good predictor of demographic performance measures for a number of Neotropical migrant birds. Although this

work provided essential baseline data, it did not provide information on the relative contribution of local and landscape factors to population growth. This work also was unable to decouple the relative contribution of habitat amount vs. habitat fragmentation on the distribution and demography of birds in managed landscapes. Achieving these goals may require diverse monitoring approaches because demographic vital rate data can only be collected on finer spatial scales while distribution, richness, and abundance data must be collected at much larger spatial scales. Regardless of scale, studies that inform how habitat quality (i.e., amount and fragmentation) shape the contributions of overall distribution, abundance and demography to population growth as well as which aspect of landscape structure are most critical to population persistence, are essential for proactive conservation. Ultimately, understanding these relative contributions can inform how resource managers allocate resources towards fine-scale habitat protection and management vs. base wide or even larger regional management strategies to conserve avian populations.

Here, we describe a multi-institutional collaboration (Smithsonian, Institute for Bird Populations, Oregon State University and US Army Engineer Research and Development Center) funded by SERDP (RC-2121) with two primary aims: 1) to validate and test the performance of three avian sampling approaches (point-counts, MAPS and intensive demography) to characterize source-sink dynamics, and 2) to determine which local and landscape factors influence distribution, demography, and overall population persistence on both DoD installations as well as in surrounding landscapes. This research was carried out at Jefferson Proving Ground (now Big Oaks National Wildlife refuge), NSA Crane, and within surrounding Indiana state forests and parks. Given the limitations of collecting intensive demographic data for multiple species, our work primarily focuses on Wood thrush (*Hylocichla mustelina*), a DoD species of concern. Where possible, we use the larger spatial scale data from point-count sampling and MAPS to assess the factors that influence demographic performance and population persistence for specific species of concern and the broader community of birds.

The report is organized into four chapters that address the projects broad objectives. Chapter one provides detailed results on the point-count and occupancy component of the research. This chapter first assesses the impact of temporary emigration on occupancy models' ability to characterize population dynamics, and second, applies occupancy models to quantify the independent effects of habitat amount, fragmentation, and their interaction on dynamic avian distribution patterns. These results will provide the DoD useful information about how to sample and model dynamic distributions of unmarked animal communities, identify local and landscape features that have positive and negative effects on forest bird communities, and provide information about occurrence "hotspots" on and around military bases for avian species of concern. Chapter two provides detailed results for MAPS constant effort mist-net monitoring. This chapter characterizes two key vital rates (survival and fecundity) for modeling population growth, compares those rates to those derived from intensive demographic monitoring, and assesses the local and landscape predictors of Wood thrush productivity. These results provide essential information on the accuracy of previously collected vital rate data on DoD installations and identify the landscape features that drive regional Wood thrush productivity. These results also provide essential information about the spatial scale of inference for MAPS measures of productivity and how they should be applied to management decisions. Chapter three reports on the intensive demographic monitoring component of the research. This chapter details a full-annual cycle integrated population model that provides key vital rates (survival, fecundity, immigration, etc.) for both multiple age classes and across the breeding and non-breeding season. This chapter

specifically addresses the role of immigration, and to a lesser extent emigration, in source-sink dynamics. Model results are used to understand the relative contribution that different vital rates make to population growth. In addition, the chapter also details the key drivers of habitat specific demography and how these variable demographic rates differentially contribute to population dynamics. These results provide the DoD an essential understanding of which vital rates drive population growth, how those processes vary with habitat quality, and details the role of breeding vs. non-breeding season population limitation. Chapter 4 is a synthesis of results from the first three chapters. This chapter specifically compares population growth estimates from the hierarchy of approaches (low resolution and effort counts to high resolution and effort intensive demography) to assess the accuracy and precision as well as the scale at which each approach can inform population dynamics. In addition, we discuss the pros and cons of each methodological approach and their utility for assessing changes in population growth. Given that self-recruitment rate is the best indicator of population persistence, this chapter reviews which local and landscape features best predict the contribution of each local Wood thrush population. Finally, we compare the results from the occupancy modeling and demographic monitoring to broadly discuss the relationships between distributional patterns and population dynamics for a suite of passerine species on DoD installations.



## **Chapter 1- Using dynamic occupancy and species distribution models to understand species sensitivity to landscape configuration**

### **Abstract**

During the breeding seasons of 2011-2014 we conducted avian point counts on two DoD installations in southern Indiana (NSA Crane and Big Oaks National Wildlife Refuge) and surrounding areas in order to identify the effects of forest structure on breeding bird distributions and temporal dynamics. Point count stations were selected to: 1) reduce correlation between the size of the forest patch in which the point was located, and the amount of forest within 2 km of the point, and, 2) adequately sample demographic plots monitored by Smithsonian Institution personnel (Chapter 3). We used a popular sampling protocol designed with the intention of allowing us to model dynamics both within and among breeding seasons with dynamic occupancy (MacKenzie *et al.* 2003) and abundance (Dail & Madsen 2011) models. These approaches rely on Pollock's (1982) robust sampling design and an assumption of site closure over repeated secondary sampling periods nested within primary sampling periods (between which dynamic rates are estimated). Initial exploration of our data led us to question whether the dynamic processes being modeled within breeding seasons in fact represented distributional shifts, or temporary movements in and out of our sample areas due to temporary emigration (TE). Thus, we first used simulated and empirical point count data to test the hypothesis that TE can confound estimates of dynamic rates within breeding seasons. Data simulations indicated that when TE occurred randomly and independently on each sampling occasion, dynamic rate estimates were highly accurate and precise. However, when secondary sampling periods were closed to TE, tests for population dynamics, and dynamic rate estimates were biased. In empirical datasets, we found evidence of population dynamics within a single breeding season for all species when primary sampling periods occurred in immediate succession (*i.e.*, 3 samples within 10 minutes). However, our results suggest that this is because estimates of population dynamics were heavily influenced by TE rates, and thus we were only able to model dynamic rates between breeding seasons.

Using dynamic occupancy models (MacKenzie *et al.* 2003) we then quantified the effects of forest patch size and forest amount on the probability of initial site occupancy, and inter-annual colonization and extinction rates for 30 species. In all models, we controlled for variability in local vegetation characteristics and edge distance to ensure that any effect sizes could be attributed to the landscape variables themselves. Initial occupancy of 16 species was significantly influenced by one or more of our landscape variables (habitat amount, patch size, or their interaction). However, landscape variables only had a significant effect on colonization rates for 6 species and extinction rates for 11 species. Further, the direction of many of these effect sizes was opposite of what would be predicted by ecological theory. There are many possible explanations for these results, the most likely of which is that defining "habitat" by forest patch boundaries is likely an oversimplification for many species.

We then used community occupancy models to investigate the impacts of local and landscape variables on community structure and composition. By modeling communities using this approach, we were able to estimate species richness while accounting for imperfect detection, identify life history traits that are more sensitive to forest loss and fragmentation, and borrow information from common species to estimate factors influencing the distribution of rare and cryptic species. Community occupancy models revealed that fragmentation did not negatively impact species richness, and in fact, had a positive effect on many species, particularly those that prefer edge habitat. However, all forest interior specialists, which tend to be of greater

conservation concern, were negatively impacted by reduced patch sizes stemming from fragmentation.

As a final step, we developed species distribution models (SDMs) for 30 species. SDMs were constructed by modeling observed point count data as a function of explanatory variables extracted from Landsat 5 TM imagery using boosted regression trees (BRTs). The BRTs for 18 of these species performed well when tested against held-out validation data ( $AUC \geq 0.7$ ), and thus we used them to produce region-wide, spatially-explicit maps of occurrence probability. These maps will be useful to DoD for identifying biodiversity hotspots, or high probability use areas for species of interest in southern Indiana. In the future, we intend to use these spatially-explicit models to refine our estimates of the effect of forest loss and fragmentation on bird distributions and dynamics.

## Objective

In this chapter, we begin by combining simulated and empirical avian point count data to investigate the impacts temporary emigration (TE) may have on dynamic population models for samples of unmarked animals. We then test for the independent effects of habitat amount, fragmentation, and their interaction on dynamic avian distribution patterns while accounting for variability in local vegetation and edge effects. Lastly, we combine our point count results with Landsat Thematic Mapper imagery to generate species distribution models for common breeding birds in southern Indiana. The goals are to: 1) provide DoD useful information about how to sample and model dynamic distributions of unmarked animal communities, 2) identify landscape features on and around military bases that have positive and negative effects on forest bird communities, and 3) provide information about occurrence “hotspots” on and around military bases for avian species that may be of DoD concern.

## Background

Habitat loss and fragmentation are some of the greatest threats to terrestrial biodiversity worldwide (Wilcove et al. 1986; Noss 1991; Pimm et al. 1995; Pimm & Raven 2000). Forests have been particularly hard hit by these processes, as 70% of the remaining forest in the world is now located within 1 km of the forest’s edge (Haddad et al. 2015). Habitat loss refers to changes in landscape composition, while fragmentation per se refers to the breaking apart of contiguous habitat (Fahrig 2003; Hadley & Betts 2016). Though these processes often occur simultaneously, they can have unique effects on species populations, and distinguishing between these two aspects of landscape structure is fundamental to metapopulation dynamic theory (Hanski & Ovaskainen 2000), reserve design, and conservation of biodiversity in managed landscapes (Lindenmayer & Fischer 2007).

The deleterious effects of habitat loss are intuitive because landscapes with less suitable area can support fewer individuals. Fragmentation, on the other hand, alters the geometry of the landscape, resulting a larger number of habitat patches that are smaller and more isolated than in contiguous landscapes (Fahrig 2003). A combination of island biogeography (MacArthur & Wilson 1963; 1967) and metapopulation (Levins 1969; Hanski 1998) theory predicts that patch occupancy rates for individual species should decrease under these conditions because smaller populations (contained by smaller patches) are more likely to go locally extinct due to stochastic events, and less likely to be re-colonized from other patches due to isolation (Hanski 1998). For decades, researchers have been examining how species are distributed across fragmented



landscapes, and to date, there is relatively little congruency between empirical presence-absence data and theoretical predictions (Prugh et al. 2008).

Multiple hypotheses have been proposed to explain this discrepancy. In their review of patch size and isolation effects on species occupancy, Prugh et al. (2008) conclude that the most likely explanation for the low predictive performance of these variables is that the patches-as-islands paradigm is often an oversimplification of terrestrial landscapes. The reasoning is two-fold. First, unlike in island-ocean systems where the edges of potential habitat are easily identifiable, terrestrial landscapes are often characterized by biotic and abiotic gradients (Austin 1985; McIntyre & Barrett 1992; Wiens 1994; McIntyre & Hobbs 1999; Manning et al. 2004; Fischer & Lindenmayer 2006). Second, habitat delineations (i.e., perceived patches or subpopulation units), as typically defined from a human perspective, may be poor categorizations at the species level. The “fragmentation model” (*sensu* Fischer & Lindenmayer 2006) generally does not recognize that landscapes are perceived uniquely by different species (McIntyre & Barrett 1992; McIntyre & Hobbs 1999; Haila 2002; Manning et al. 2004; Fischer & Lindenmayer 2006; Fahrig 2013; Betts et al. 2014), which is a concept widely accepted and rooted in niche theory (Grinnell 1917; Hutchinson 1957). As such, generalized measurements of habitat configuration, as defined by humans and applied to multiple species, would certainly incorporate errors of omission or commission on a species-by-species basis.

On the other hand, human-defined patch boundaries should be reasonable habitat delineations for some species. For instance, Bender et al. (1998) found that patch size had a strong effect on population declines for habitat specialists, but not for habitat generalists. Thus, when a species’ habitat requirements generally align with habitat designations, theory would still predict negative effects of fragmentation above and beyond habitat loss. Fahrig (2013), however, recently argued that the effects of habitat loss overwhelm the effects of fragmentation per se, suggesting that in many cases the effects of patch size and isolation on species distributions could both be readily explained by habitat amount. Alternatively, theoretical models suggest that fragmentation should only influence species distributions below critical thresholds in habitat amount (Lande 1987; With & King 1999). Indeed, in his review of studies investigating fragmentation effects on birds and mammals, Andren (1994) found that fragmentation per se only has a negative effect on species distributions once the amount of habitat in the landscape drops below 30%. Above this threshold, the primary effect of fragmentation occurs through loss of habitat (Andren 1994; Fahrig 2003; Fahrig 2013).

Thus, despite thousands of studies, numerous questions remain regarding the effects of habitat loss and fragmentation on species distributions and dynamics. One major reason for this is that, in many studies, habitat loss and fragmentation are confounded either conceptually or statistically. In her landmark paper, Fahrig (2003) highlighted the necessity of distinguishing between these two processes and offered suggestions for how to do so in both experimental and observational studies. In the more than a decade since this paper was published, only 18% of fragmentation studies control for the effects of habitat amount when investigating fragmentation effects (Hadley and Betts 2016). Further, the majority of authors failed to define loss and fragmentation separately, instead regarding them as a single, indistinguishable process (Hadley and Betts 2016). Such studies contribute little to our understanding of how fragmentation per se influences populations. In addition, the process of fragmentation influences landscapes in multiple ways, such as by reducing patch sizes, increasing patch isolation, increasing the edge-area ratio of remnant patches, and altering microclimatic conditions (Saunders et al. 1991; Fahrig 2003). Thus,

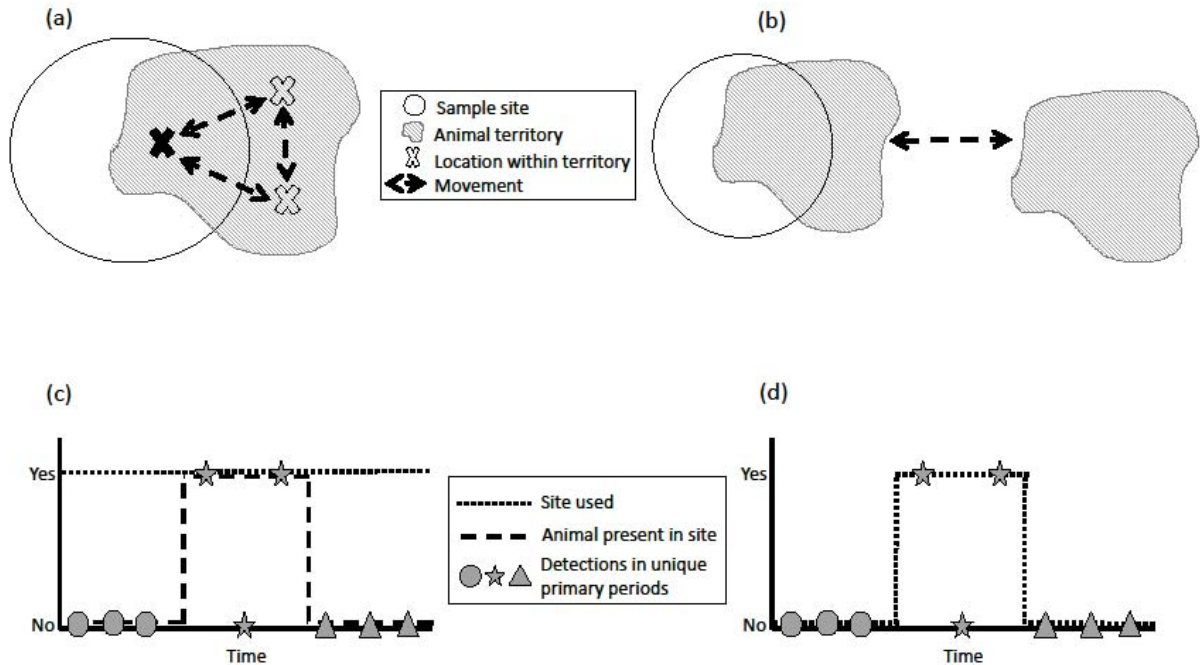
even in studies where the effects of fragmentation per se can be independently discerned, researchers often fail to identify the specific mechanism influencing distribution patterns.

Lastly, under the patches-as-islands paradigm, theory predicts that changes in species distributions should be governed by local colonization and extinction events (MacArthur and Wilson 1963; 1967; Levins 1969; Hanski 1998). However, many fragmentation studies fail to explicitly demonstrate the relationship between these dynamic processes and resulting species distribution patterns (Wilson et al. 2016). Recently developed models (*e.g.* MacKenzie et al. 2003; Dail and Madsen 2011) rely on *Pollock's robust sampling design* (Pollock 1982) to estimate dynamics of unmarked populations while accounting for imperfect detection. This approach requires repeated samples within primary periods in which sites are assumed closed to distributional changes, allowing estimation of dynamic rates between these periods. Recent studies have demonstrated that commonly used sampling protocols for birds (Rota et al. 2009; McClure & Hill 2012), salamanders (Otto et al. 2013), anurans (Kendall et al. 2013), and insects (Bried & Pellet 2012) violate the repeated sampling closure assumption, leading to widely touted recommendations that repeated samples be conducted very close together in time (MacKenzie & Royle 2005; MacKenzie 2005; Rota et al. 2009; Kendall et al. 2013). However, under this approach, estimates of population dynamics may be confounded with rates of *temporary emigration* (TE; reversible changes in sampling availability), for instance, due to mismatches between the spatial scale of sampling and that of sampled animal territories (Figure 1.1; Nichols et al. 2009; Chandler et al. 2011; Efford & Dawson 2012). To date, the degree to which TE can confound estimates of true population dynamics (births, deaths, and territorial changes), has not been tested.

## **Materials and Methods**

### **Point Count Locations**

We selected point count locations using two different approaches to accommodate the diverse project goals. The first set of point count stations are deemed *forest patch stations*. For these, we began by digitizing all forest patches either completely or partially contained within the boundaries of all publicly owned lands (and some privately-owned lands we had access to) within 1 hour's drive from our field houses (Loogootee, IN and Madison, IN). These locations



**Figure 1.1** An example of the two processes that can lead to closure violations for mobile animals. Temporary emigration stemming from within-territory movements (a) can complicate estimation of changes in site use resulting from births, deaths, or dispersal (b). In (c), for instance, all samples within a single primary period (denoted by identical symbols) occur so close in time that TE only occurs between primary periods. The resulting detection history (000 101 000) may be misinterpreted as an unused site that is colonized, then abandoned (d), even though the site is used continuously.

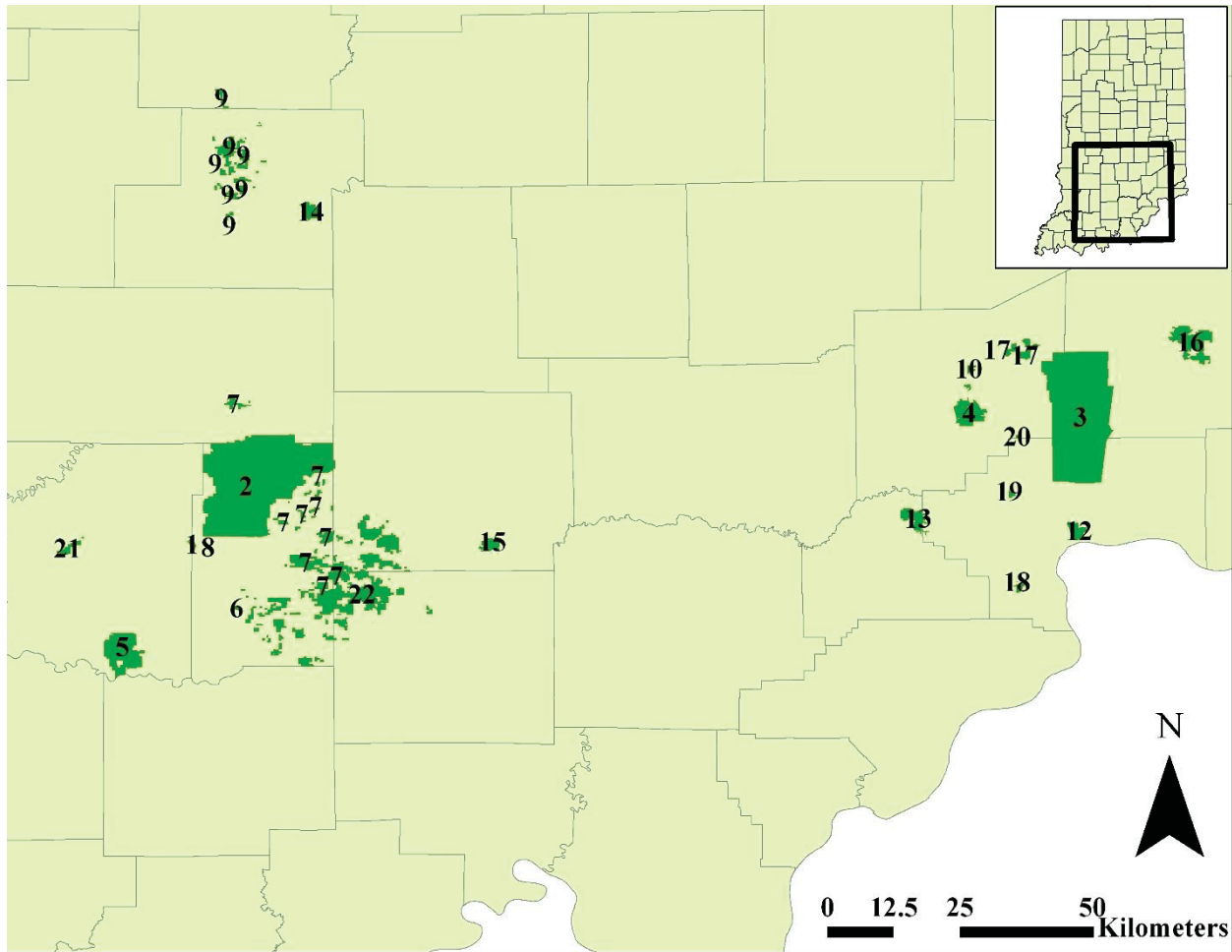
were selected due to their proximity to two large DoD installations, NSA Crane, and Big Oaks National Wildlife Refuge. We then used a stratified random sampling approach to select point count station locations while minimizing correlation between forest patch size and the amount of forest within 2 km (habitat amount) of the stations. Habitat amount was calculated using the 2011 USGS National Land Cover Database (Homer et al. 2015). We selected 202 unique forest patches ranging in size from 0.89 ha to 22,800 ha (median 12.02 ha), and placed between 1 and 10 point count stations in each, with smaller patches receiving fewer points. In patches with multiple points, the first was placed approximately 50 m from the edge of the forest, and additional points were placed at 250 m intervals along a transect extending towards the center of the patch. In all, we selected 490 point count stations on 22 different publicly and privately owned properties (Table 1.1; Figure 1.2), and habitat amount ranged from 11.22% to 99.81% (median 63.51%). Pearson's correlation between habitat amount and log-transformed patch size was  $r = 0.22$ . This placement method allowed us to 1) discern the independent effects of forest loss and fragmentation on bird species distributions, and 2) to evaluate whether any effects of patch size on distribution patterns could be explained by edge distance alone.

The second set of points are deemed *demographic plot stations*. These were placed systematically in a 200 m grid pattern on all demographic plots outlined by Smithsonian Institution personnel (Chapter 3). In 2011, we established 164 point count stations on demographic plots (8-19 per plot; Table 1.1; Figure 1.2). In 2012, some demographic plots were expanded, and another 29 point count stations were added to cover the supplemental area (193 total point count stations

on demographic plots; 8-28 per plot). Selection and placement of all point count locations was done using ArcGIS v. 10.2.2.

**Table 1.1** Distribution of forest patch and demographic plot point count stations across public and private lands sampled during the breeding seasons of 2011-2014. Note that different numbers of points were sampled in each year (see text above). The column labeled “Number” can be used to reference geographic locations of each property in Figure 1.2.

Owner (Manager)	Number	Property	Forest Patch	Demographic Plot	Total
Davies-Martin Parks and Rec. Dept.	1	West Boggs Park	4	0	4
DOD	2	NSA Crane	151	67	218
DOD (USFWS)	3	Big Oaks NWR	25	64	89
IDNR (Fish & Wildlife)	4	Crosley Fish & Wildlife Area	26	0	26
	5	Glendale Fish & Wildlife Area	75	0	75
	6	Hindostan Falls Public Fishing Area	4	0	4
IDNR (Forestry)	7	Martin State Forest	8	17	25
	8	Mt. Calvary Wildlife Management Area	4	0	4
	9	Owen-Putnam State Forest	5	15	20
	10	Selmier State Forest	5	0	5
IDNR (Nature Preserves)	11	Violet and Louis J. Calli Sr. Nature Preserve	5	0	5
IDNR (State Parks and Reservoirs)	12	Clifty Falls State Park	9	0	9
	13	Hardy Lake	53	0	53
	14	McCormick's Creek State Park	0	15	15
	15	Spring Mill State Park	2	15	17
	16	Versailles State Park	25	0	25
Purdue University	17	Southeast Purdue Agricultural Center	15	0	15
The Nature Conservancy	18	Chelsea Flatwoods Nature Preserve	9	0	9
	19	Pennywort Cliffs	7	0	7
	20	Sarah Lewis Guthrie Memorial Woods Nature Preserve	3	0	3
	21	Thousand Acre Woods Nature Preserve	16	0	16
U.S. Forest Service	22	Hoosier National Forest	39	0	39
Total			490	193	683



**Figure 1.2** Locations of all publicly and privately owned properties on which we conducted point count surveys during the breeding seasons of 2011-2014. Property names can be identified by referencing the "Number" column in Table 1.1.

### Avian Sampling

In 2011-2013 we conducted 3 avian point counts at each established station, and repeated visits to the same location were separated by approximately 2 weeks. In 2014 we only sampled the 193 demographic point count stations. These were also sampled 3 times, but the first two visits to each station were conducted within two mornings of each other, and the third visit was conducted 15 to 19 (median 17) days after the first.

All point counts were conducted between 29 May and 18 July in each year, and between 30 minutes before sunrise and 4 hours after sunrise in suitable weather conditions. We used a popular sampling protocol (*e.g.*, Betts et al. 2008; Rota et al. 2009; McClure and Hill 2011; Otto & Roloff 2012) where counts lasted 10 minutes and were divided into 3:20 intervals, during each of which observers recorded all birds seen or heard within 100 m.

### Vegetation Sampling

We conducted vegetation surveys at each location in both 2011 and 2013, and additional vegetation surveys in 2012 only at sites that had been visibly disturbed (*e.g.*, by forestry practices), or newly established since 2011. During a vegetation survey, we established one 5 m radius circle centered on the point count station, and another centered 30 m from the point count station in a

randomly chosen cardinal direction. Within each vegetation survey plot we measured five broad vegetation metrics: 1) Frequency of trees in different size classes, 2) canopy cover, 3) shrub cover, 4) vertical foliage density, and 5) leaf litter depth. Frequency of tree size classes was measured with a 2 BAF forester's prism and a tree DBH tape. All trees with the survey plot were categorized as either deciduous or coniferous and placed into one of 4 DBH size classes (1-5 cm, 6-20 cm, 21-30 cm and > 30 cm). We measured canopy cover using 10 samples from an Emlen tube (Emlen 1966). We measured shrub cover as any foliage associated with woody vegetation < 2m above the ground. Four ocular estimates of percent cover were taken within each plot (< 0.5m, 0.5-1m, 1-2m and > 2m). Vertical foliage density was measured at four perimeter points in each cardinal direction. We specifically, used a 6m extendable pole that was sub-divided into 0.25m increments. Within each increment, we recorded whether or not any live woody vegetation (including stems, leaves, needles, branches, and tree trunks) contacts the pole. We measured leaf-litter depth at the same cardinal direction perimeter points as those used for vertical foliage density. At each point, a ruler was inserted into the leaf-litter until it reached the dirt and the depth of litter was measured to the nearest 0.5 cm. All metrics were averaged among the two plots at a point count station, and metrics measured in 2011 were also associated with 2012 for sites where no vegetation survey was conducted that year.

### **Effects of Temporary Emigration on Estimates of Population Dynamics**

Repeated sampling approaches (*e.g.*, MacKenzie et al. 2002; 2003; Royle and Nichols 2003; Royle 2004; Dail and Madsen 2011) are widely used in wildlife studies because they allow researchers to quantify species distributions while simultaneously accounting for imperfect detection. When using these methods, it is typically assumed that samples of spatially discrete units take place at a single instant in time, allowing for instantaneous estimates of abundance or occupancy (Nichols et al. 2009; Chandler et al. 2011). However, as numerous authors have pointed out, the number of individuals exposed to sampling at any instant in time is often a subset of the number of individuals that use the site, also known as the site's *superpopulation* (Kendall et al. 1997; Kendall 1999; Nichols et al. 2009; Chandler et al. 2011; O'Donnell et al. 2015). Each member of a site's superpopulation has some non-zero probability of being exposed to the sampling effort, but individuals not exposed during a realized moment in time are called *temporary emigrants*.

If we define the superpopulation of a site as  $N_0$ , and the probability of any individual being available for sampling as  $p_a$  (the complement of the TE rate), then repeated sampling approaches typically estimate  $N_0 p_a$ , abundance at a specific point in time (Nichols et al. 2009; Riddle et al. 2010). However, when the closure assumption is relaxed such that the superpopulation size remains constant, but the number of individuals available for sampling can change in a non-Markovian way between visits, repeated sampling (Royle & Nichols 2003; Royle 2004) actually estimates  $N_0$  (Kendall 1999; Nichols et al. 2009). Similarly, researchers can estimate *use* rather than occupancy from repeated presence/absence sampling under these conditions (MacKenzie et al. 2002; MacKenzie & Royle 2005). Under this approach, detection probability is estimated as the product of  $p_a$  and  $p_d$  where  $p_d$  is the probability of detection given availability (Kendall 1999; Nichols et al. 2009).

### **Simulated Data**

To investigate the effects of TE on estimates of population dynamics, we began with a series of simulated datasets. We began our simulations with two explicit assumptions: 1) TE



occurs over finer time scales than population dynamics; and 2) the researcher is interested in quantifying population dynamics (as we are in this study). We then simulated presence/absence and count datasets under two different robust-design sampling scenarios (Pollock 1982), one in which the researcher estimates site use ( $\psi_0$ ) or superpopulation size ( $\lambda_0$ ), and one aimed at quantifying occupancy ( $\psi = \psi_0 p_a$ ) or abundance ( $\lambda = \lambda_0 p_a$ ) during each primary period.

Each dataset contained 500 sites with nine sampling occasions. In all datasets, use or superpopulation size was allowed to change every third sampling period. For presence/absence datasets, we simulated the initial use ( $\psi_0$ ) of each site from a Bernoulli distribution with probabilities of 0.3 or 0.7. Extinction of used sites was determined by a random draw from a Bernoulli distribution with probabilities of  $\varepsilon = 0.0, 0.2$ , or  $0.4$ . Colonization of unused sites was determined by a draw from a Bernoulli distribution with probabilities of  $\gamma$  where  $\gamma$  was calculated so the expected value of the site use rate remained constant. In abundance datasets, the initial site superpopulation ( $\lambda_0$ ) of each site was drawn from a Poisson distribution with mean parameters of 1 or 2. The number of individuals continuing to use a site (apparent survival) during each subsequent primary period was determined by a random draw from a binomial distribution with probabilities of  $\omega = 1, 0.8$ , or  $0.6$ . Recruitment events were drawn from a Poisson distribution with a mean parameter of  $\phi$ , where  $\phi$  was again calculated so the expected superpopulation size remained constant. Note that here we are defining colonization and extinction as changes in site use, independent of temporary changes in availability. Similarly, recruitment and apparent survival are defined as changes in superpopulation size. Thus, the parameters  $\gamma$ ,  $\varepsilon$ ,  $\phi$ , and  $\omega$  represent the dynamic population rates of interest in the study.

On any given sampling occasion, whether any individual (count) or at least one individual (presence/absence) using the site was available for detection was determined by random draws from binomial or Bernoulli distributions (respectively) with probabilities of  $p_a = 0.5$  or  $0.8$ . Here,  $p_a$  represents the complement of the TE rate. In the *use* and *superpopulation* sampling scenarios, availability was independent on each sampling occasion, while in the *occupancy* and *abundance* scenarios availability could only change every third visit, allowing for instantaneous estimates of distributions within primary periods (Kendall 1999). Lastly, whether each available individual (count) or at least one available individual (presence/absence) was detected was determined by a draw from a binomial or Bernoulli distribution with probabilities of  $p_d = 0.5$  or  $0.8$ . In all, we simulated 1000 presence/absence, and 1000 count datasets for each combination of 24 parameter values under each sampling scenario. All datasets were generated using R (v. 3.1.2).

We fit static and dynamic presence/absence (MacKenzie *et al.* 2002; MacKenzie *et al.* 2003) or count (Royle 2004; Dail & Madsen 2011) models to each of the respective 48,000 datasets using `occu()`, `colext()`, `pcount()`, and `pcountOpen()` functions in the *unmarked* R package (v. 0.10-6; Fiske & Chandler 2011). Static models assumed no population dynamics between any visits and open models allowed distributions to change after every third visit. We assumed site abundance was Poisson distributed in all count models and that there was no relationship between recruitment rate and apparent survival in dynamic count models.

We then tested for evidence for population dynamics in each dataset by comparing static and dynamic models. Static presence/absence or count models are special cases of their dynamic counterparts where dynamic parameters are constrained to be either zero or one. To formally test site closure, we calculated a test statistic as  $T = -2\ln(\Lambda)$  where  $\Lambda$  is the ratio of the maximized likelihood for the static model to that of the dynamic model. Because the null hypothesis here is that the dynamic parameters are on the boundaries of their parameter spaces, this test does not meet the regularity conditions for a likelihood ratio test. Instead, this test statistic asymptotically

approaches a mixture  $\chi_0^2$ ,  $\chi_1^2$ , and  $\chi_2^2$  distributions with mixing proportions equal to  $0.5-\delta$ ,  $0.5$ , and  $\delta$ , where  $\delta$  was calculated from the Hessian matrix of the dynamic model (Self & Liang 1987; Dail & Madsen 2011). When  $\delta$  could not be estimated ( $< 1\%$  of comparisons), it was fixed at  $0.5$  to minimize the probability of rejecting the null (static) model. We accepted a P-value of  $< 0.05$  as evidence for population dynamics.

For each combination of parameters under each sampling scenario we calculated the percentage of time the correct model was selected, and compared parameter estimates from the selected models with the values used to generate the data. Again, we assumed the researcher is interested in quantifying births, deaths, and dispersal, so the dynamic model was deemed “incorrect” when  $\gamma = 0$  and  $\varepsilon = 0$  in simulated presence/absence datasets, or when  $\phi = 0$  and  $\omega = 1$  in simulated count datasets. Similarly, we compared model estimates of the dynamic rates with those governing changes in site use ( $\gamma$  and  $\varepsilon$ ) or superpopulation size ( $\phi$  and  $\omega$ ). We calculated bias as the parameter estimate minus its true value, averaged over all 1000 datasets. Variance was calculated among the estimates themselves, and mean squared error (MSE) as the sum of the variance and the squared bias. We disregarded parameter estimates from models with non-invertible Hessian matrices ( $< 2\%$  of fitted models).

## Empirical Case Study

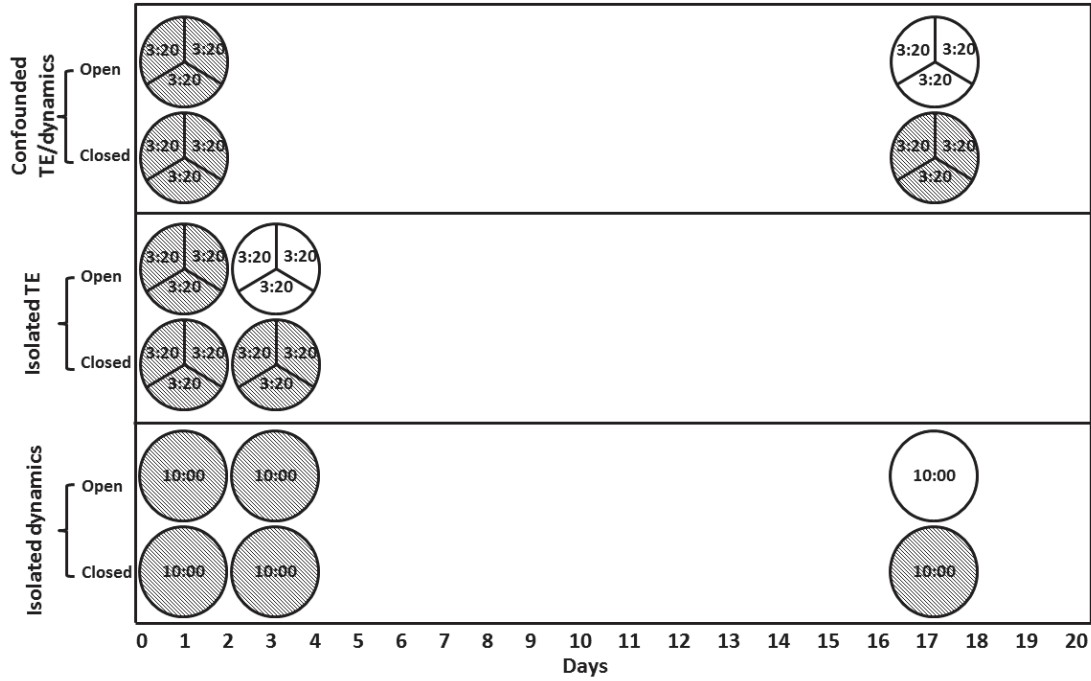
We used only the data collected on birds within 50 m of the 193 demographic plot point count stations in 2014 for this analysis. As mentioned above, we conducted two visits to each station within two mornings of one another, and a third visit 15 to 19 (median 17) days after the first. Counts lasted 10 minutes and were divided into 3:20 intervals. For clarity, we will refer to day-specific 10-minute point counts as *visits* and repeated 3:20 samples within each visit as *intervals*.

We constructed three unique presence/absence and count datasets from the resulting point count data (Figure 1.3), and label them based on the process we assume is being isolated between primary periods. Because our survey sites were stationary (50 m radius circles), TE could result from individuals moving within their territories, but outside of the sample space (Figure 1.1). In addition, births, deaths, and dispersal events could be possible over the course of our 19 day sampling period.

The first dataset combined only the first and third visits to each station, but included the six repeated intervals (three per visit). Intervals were treated as secondary periods nested within primary periods (site visits) when fitting dynamic models. Such a protocol might be used when a researcher is interested in estimating changes in occupancy or abundance rather than use or superpopulation size (MacKenzie & Royle 2005). Under this design, we assumed secondary periods were closed to both dynamics and TE, and therefore both processes only occurred between primary periods. We refer to this data configuration as the *confounded TE/dynamics* dataset.

The second dataset was similar to the first, but used only the first and second visits (with six repeated intervals). Again, we assumed that secondary periods were closed to both dynamics and TE. However, because the two visits in this dataset were separated by no more than 48 hours, we assumed that the only dynamic process occurring between primary periods was TE. We refer to this data configuration as the *isolated TE* dataset.





**Figure 1.3** A schematic outlining the structure of the three occupancy and abundance datasets constructed from repeated point counts at 193 locations in southern Indiana in the summer of 2014. Circles represent 10-minute site visits, some of which were split into 3:20 subintervals. Circles or parts of circles shaded similarly were considered part of the same primary sampling period.

The final dataset combined all three visits and ignored the repeated intervals; this represented a sampling design for estimating changes in use or superpopulation sizes of unmarked populations (Mackenzie & Royle 2005). Here we assumed the temporal duration (24-48 h) between the first two visits was short enough to be closed to population dynamics, but open to temporary emigration. Treating these first two visits as a single primary sampling period ensured that the probability of detection was estimated as  $p_{\text{apd}}$  (Nichols et al. 2009), allowing tests of true population dynamics between primary periods. We refer to this data configuration as the *isolated dynamics* dataset.

We limited our analyses to only those species detected on > 20% of sample sites (Table 2). Using the same approach described above, we tested for population dynamics in each of these 57 datasets (three per species) by comparing presence/absence (MacKenzie et al. 2002) and count (Royle 2004) models that assumed site closure over all samples to those that allowed distributions to change between primary periods (MacKenzie et al. 2003; Dail & Madsen 2011). In each model, time of day and observer were included as covariates for detection probability, but for simplicity, distribution and dynamic parameters were modeled as constants. We assumed the response variable was Poisson distributed in all count models, and no relationship between recruitment rate and apparent survival probability for dynamic count models. We compared dynamic model parameter estimates within species and across datasets using paired t-tests to investigate how sampling situations influence estimates. All analyses were conducted using the `occu()`, `colext()`, `pcount()`, and `pcountOpen()` functions in the *unmarked* package (v. 0.10-6) in R (v. 3.1.2).

Using datasets analogous to those we deemed confounded TE/dynamics, several researchers (e.g., Betts et al. 2008; Rota et al. 2009; McClure & Hill 2012) concluded there was

substantial evidence for within-breeding season territorial changes in bird communities. Thus, analysis of our confounded TE/dynamics datasets allowed us to replicate these results. Analysis of the isolated TE and isolated dynamics datasets provided the opportunity to evaluate how these conclusions change when the movement being modeled represented each process independently.

### Effects of Fragmentation on Avian Distributions and Dynamics

To investigate the independent effects of habitat loss and fragmentation on avian distribution patterns, we used the data collected from the 490 forest patch point count stations over 3 years (2011-2013). We eliminated all swifts, swallows, migrants, raptors, hummingbirds, and nocturnal or crepuscular species from consideration because our methods were not designed to sample these groups. Because our estimates of “habitat” were defined as forest cover, we also eliminated waterbirds, and habitat generalists (i.e., those that frequently utilize non-forested areas) from consideration. We then selected the 30 most widely-distributed remaining species and developed species-specific dynamic occupancy models using the approach developed by MacKenzie et al. (2003).

We began model construction by conducting a principal components analysis on the 5 standardized vegetation variables measured at the site-by-year level. We took this approach because: 1) we were not explicitly interested in quantifying the effects of local vegetation on species distributions, but rather in accounting for it; and 2) it allowed us to reduce the number of explanatory variables in our models. The first 3 principal components explained 77% of the variability in our local vegetation data (see results), and thus we were able to eliminate two explanatory variables while still accounting for substantial local variability.

As mentioned above, dynamic occupancy models utilize Pollock’s (1982) robust sampling design to estimate distributions and changes in distributions as a function of habitat features while simultaneously accounting for imperfect detection. We assumed that sites were closed to changes in occupancy over the 3 repeated visits within a breeding season, and allowed occupancy status of a site to change between years. The model specifies that site specific occupancy for the species of interest at site  $j = 1, 2, \dots, 490$  in year  $k = 1, 2, 3$  (denoted  $Z_{j,k}$ ) is 1 if the species uses site  $j$  in year  $k$ , and 0 otherwise. The model assumes that  $Z_{j,1} \sim \text{Bernoulli}(\psi_{j,1})$  where  $\psi_{j,1}$  is the probability of initial occupancy for the species at site  $j$  in year 1. We then modeled the initial occupancy rate as a function of habitat features using the following logit function:

$$\text{logit}(\psi_{j,1}) = \beta_0 + \beta_1 * PC1_{j,1} + \beta_2 * PC2_{j,1} + \beta_3 * PC3_{j,1} + \beta_4 * \text{edge.dist}_j + \beta_5 * \log(\text{patch.size}_j) + \beta_6 * \text{amount}_j + \beta_7 * \log(\text{patch.size}_j) * \text{amount}_j$$

In this model: PC1, PC2, and PC3 are the values of the first 3 local vegetation principal components measured at the point-by-year scale; edge.dist is the distance from the point count station to the nearest forest patch edge; patch.size is the size (ha) of the forest patch in which the point was located; and amount is the proportion of the landscape within 2 km of the point comprised of forest. We were not able to include a patch-level random effect in our analyses because there was only 1 point in 89 (44%) of the patches, making it impossible to separate point-level variability from patch-level variability. For subsequent years ( $k = 2, 3$ ), the model assumes  $Z_{j,k} \sim \text{Bernoulli}(\psi_{j,k})$  where

$$\psi_{j,k} = (1 - Z_{j,k-1}) * \gamma_j + Z_{j,k-1} * (1 - \varepsilon_j)$$

$$\text{logit}(\gamma_j) = \gamma_0 + \gamma_1 * \log(\text{patch.size}_j) + \gamma_2 * \text{amount}_j + \gamma_3 * \log(\text{patch.size}_j) * \text{amount}_j + \gamma_4 * \text{edge.dist}_j$$

$$\text{logit}(\varepsilon_j) = \varepsilon_0 + \varepsilon_1 * \log(\text{patch.size}_j) + \varepsilon_2 * \text{amount}_j + \varepsilon_3 * \log(\text{patch.size}_j) * \text{amount}_j + \varepsilon_4 * \text{edge.dist}_j$$

Here  $\gamma_j$  represents the probability of site  $j$  becoming colonized given that it was not previously occupied, and  $\varepsilon_j$  represents the probability of site  $j$  being vacated given that it was previously occupied. Thus, initial occupancy in 2011 is being modeled as a function of local and landscape level habitat variables, while occupancy in years 2012 and 2013 is modeled as a Markovian process where the occupancy state is dependent on the occupancy state in the previous year. This model, in conjunction with our study design, allowed us to test the independent effects of patch size, habitat amount, and their interaction on distribution patterns and dynamic population rates simultaneously.

In cases where the species was directly observed,  $Z_{j,k}$  is known, but because individuals are often imperfectly detected,  $Z_{j,k}$  is a latent variable when no individual was observed. Thus, the model uses the repeated observations of presence and absence in each year at each site to adjust our estimates to account for imperfect detection. The observations are denoted  $y_{j,k,l}$  where  $l = 1, 2, 3$ , and the observation component of the model is specified as

$$y_{j,k,l} \sim \text{Bernoulli}(Z_{j,k} * p)$$

$$\text{logit}(p_i) = \alpha_0_m * I(\text{observer}_m)_{j,k,l} + \alpha_1 * \text{time}_{j,k,l} + \alpha_2 * \text{Julian}_{j,k,l}$$

Where  $\alpha_0$  is an observer-specific intercept ( $m = 1, 2, \dots, 19$ ), time is the number of minutes passed since midnight, and Julian is the Julian date of the year. Under this formulation, an individual species can only be detected when present. All dynamic occupancy models were constructed in R v. 3.2.2 using the `colext()` function in the *unmarked* package (Fiske & Chandler 2011), and all explanatory variables were scaled with mean of 0 and standard deviation of 1 before inclusion in the model to increase the efficiency of the estimation process.

### Effects of Fragmentation on Avian Distribution and Richness

While the dynamic occupancy models described above allowed us to identify the effects of landscape features on dynamic processes for each species individually, there are a couple of downsides to this analysis approach. First, the theoretical underpinnings of landscape conservation theory relate community distributions to landscape features, rather than individual species (MacArthur and Wilson 1963; 1967). Secondly, it ignores life history relationships between species that may be useful in predicting sensitivity to fragmentation. For instance, habitat specialists tend to be much more sensitive to patch size (Iida and Nakashizuka 1995, Bender et al. 1998, Lawesson et al. 1998, Cook et al. 2002, Godefroid and Koedam 2003, Kolb and Diekmann 2004, Puttaker et al. 2013) and other fragmentation effects than habitat generalists (Carrara et al. 2015, Blandón et al. 2016, Khimoun et al. 2016; but see Ruiz-Gutierrez et al. 2010, Fahrig 2017). Lastly, we were unable to identify variables limiting distributions of rare or cryptic species due to the paucity of data, and these species are often of greatest conservation concern (Samu et al. 2008). Thus, we also analyzed these data using a recently developed community occupancy modeling

approach (Dorazio and Royle 2005, Kéry and Royle 2008, Zipkin et al. 2009, Iknayan et al. 2014) that allowed us to explicitly estimate factors influencing distribution and detectability of all species of interest simultaneously. For this analysis, we processed the point count data by removing all species that do not breed in the region (i.e., transient migrants), and those species poorly sampled by point count methodology (i.e., raptors, waterbirds, swifts and swallows, nocturnal and crepuscular species, hummingbirds, and game birds). We classified the remaining species into four habitat groups; forest interior specialists, forest edge specialists, forest generalists, and habitat generalists. Classifications were made by a committee of expert ornithologists familiar with the local avifauna and by consultation with the Birds of North America species accounts (Rodewald 2015). We excluded habitat generalists from further analyses.

We fit a temporally-dependent, Bayesian community occupancy model to the point count data for the remaining species. Community occupancy models estimate species-specific occupancy and detection parameters within a hierarchical framework where those estimates are related through community-level hyper-parameters (Dorazio and Royle 2005, Kéry and Royle 2008, Zipkin et al. 2009). The full advantages of such a modeling approach are detailed elsewhere (Gelman and Hill 2007, Dorazio and Royle 2005, Kéry and Royle 2008, Royle and Dorazio 2008, Zipkin et al. 2009, Tingley and Bessinger 2013, Iknayan et al. 2014), but we chose it for three primary reasons. First, we were able to explicitly model detection probabilities, thereby avoiding biases associated with individuals that may have been present but undetected. Second, we were able to include all species of interest in the analysis (even rare species) because the community hyper-parameters allow borrowing of information from more common species (Royle and Dorazio 2008, Zipkin et al. 2009, Iknayan et al. 2014, Yamura et al. 2016). Lastly, we were interested in the estimates of the community hyper-parameters themselves to help summarize the differences in mean response between habitat groups.

In our model  $y_{hijklm}$  represents the observed detection information, taking a value of 1 if species  $i$  in habitat group  $h$  was detected in patch  $j$  at site  $k$  during survey  $m$  of year  $l$ , and 0 otherwise. We assumed  $y_{hijklm} \sim \text{Bernoulli}(Z_{hijkl} * p_{hijklm})$  where  $Z_{hijkl}$  represents the true species-specific occurrence state, and  $p_{hijklm}$  represents the species-specific probability of detection at the site during the sampled moment in time. Note that while detection probability can vary within a single year, this model specification assumes that sites are closed to changes in occupancy within a breeding season (about 7 weeks in our study). This assumption is standard in occupancy modeling (MacKenzie et al. 2002), and is likely reasonable for most of our breeding species. We assumed that  $Z_{hijkl} \sim \text{Bernoulli}(\psi_{hijkl})$ , and incorporated covariate effects on occupancy ( $\psi_{hijkl}$ ) and detection ( $p_{hijklm}$ ) probabilities into the model on the logit scale.

We expected that detection probability for most species would decline with increasing Julian date (Julian), and that increasing tree basal area (tree) would reduce the ability of observers to see and hear birds. Thus, detection probabilities were modeled as

$$\text{logit}(p_{hijklm}) = \alpha_{0hi} + \alpha_{1hi}\text{Julian}_{jklm} + \alpha_{2hi}\text{tree}_{jkl}$$

Note that unlike above, we did not include time of day or observer identity in these models due to model convergence issues. We modeled occupancy probability as a function of the local vegetation principal components (PC1-3), edge distance (edge.dist), log-transformed patch size (patch.size), amount of forest within 2 km (amount), and an interaction between log-patch.size and amount. In order to account for autocorrelation between points within the same patch, we included a unique random patch effect (patch) for each habitat group in each year. Ideally, we would have

included species-specific random patch effects in the model, but this simply was not possible due to the fact that 44% of patches contained only 1 point, and our modeling approach was unable to parse variability between site level and patch level intercept terms. Thus, in the first year ( $l = 1$ ), we modeled occupancy probability as

In subsequent years, we assumed that the covariate effects remained constant, but that occupancy

$$\begin{aligned} \text{logit}(\psi_{hijk1}) = & \beta_{0hi} + \text{patch}_{hjl} + \beta_{1hi}PC1_{jk1} + \beta_{2hi}PC2_{jk1} + \beta_{3hi}PC3_{jk1} \\ & + \beta_{4hi}\text{edge.dist}_{jk} + \beta_{5hi}\log(\text{patch.size}_{jk}) + \beta_{6hi}\text{amount}_{jk} \\ & + \beta_{7hi}\log(\text{patch.size}_{jk}) * \text{amount}_{jk} \end{aligned}$$

$$\begin{aligned} \text{logit}(\psi_{hijkl}) = & \gamma_{0hi} + \gamma_{1hi}Z_{hijk(l-1)} + \text{patch}_{hjl} + \beta_{1hi}PC1_{jkl} + \beta_{2hi}PC2_{jkl} \\ & + \beta_{3hi}PC3_{jkl} + \beta_{4hi}\text{edge.dist}_{jk} + \beta_{5hi}\log(\text{patch.size}_{jk}) \\ & + \beta_{6hi}\text{amount}_{jk} + \beta_{7hi}\log(\text{patch.size}_{jk}) * \text{amount}_{jk} \end{aligned}$$

probability was dependent on occupancy in the previous year. Thus, for  $l > 1$ ,

where  $\gamma_{1hi}$  is a species-specific autologistic parameter (Royle and Dorazio 2008). On a more intuitive level,  $\gamma_{1hi}$  represents the change in the occupancy intercept if the site was occupied the previous year. Note that in this analysis we are no longer explicitly modeling changes in occupancy between years as a function of covariates. The advantage of this approach is that we increase our power to detect covariate effects on occupancy itself. We standardized all covariates with a mean of zero and standard deviation of one before inclusion to assist with model convergence.

We expected that species in the same habitat group would respond to occupancy covariates similarly. However, we did not expect that the effects of detection covariates or patch effects would vary in any systematic way between habitat groups. Thus we specified parameter-specific hyperdistributions for the effects of each covariate in the following way:

$$\begin{aligned} \theta_{hi} \sim & \text{Normal}(\mu_{\theta,h}, \sigma_{\theta,h}^2), \quad \text{for } \theta = \beta_0 - \beta_7, \gamma_0, \text{ and } \gamma_1 \\ \theta_{hi} \sim & \text{Normal}(\mu_{\theta}, \sigma_{\theta}^2), \quad \text{for } \theta = \alpha_0 - \alpha_2 \\ \text{patch}_{hjl} \sim & \text{Normal}(0, \sigma_{\text{patch}}^2) \end{aligned}$$

Initial data exploration indicated low evidence for a significant patch.size-by-amount interaction for most species, and thus we also fit a second model as described above that excluded this interaction term. We fit both models in JAGS (Plummer 2003) using the jagsUI v 1.4.2 package (Kellner 2016) within the R v 3.1.2 programming language. JAGS is a Bayesian analysis program used for fitting hierarchical models via Markov Chain Monte Carlo (MCMC) simulation. We specified vague priors for all community hyper-parameters;  $\mu$  values were distributed normally with a mean of 0 and variance of 1000 while  $\sigma^2$  values had a uniform (0, 5) distribution. For each model we ran three MCMC chains for 400,000 iterations with a burn-in of 200,000 and thinned by 100. This left us with 6,000 estimates from the posterior distribution across all chains. We assessed model convergence by visually inspecting traceplots, and ensuring the Gelman-Rubin statistic for all monitored parameters was less than 1.1 (Gelman et al. 2004). We assessed model fit using a Bayesian p-value approach (Gelman et al. 2004, Kéry and Royle 2016).



Because all species are detected imperfectly, point-level species richness could not be directly observed. As a result, our model does not explicitly examine the relationship between richness and covariates. Instead, we inferred these relationships by examining predicted species richness as an emergent value from the model. For each of the 6,000 posterior draws, we first calculated predicted probability of occupancy for each species by varying the values of patch.size or amount, and holding all other covariates constant at their means. We then calculated predicted richness for the entire community and for each habitat group separately by summing these values at each iteration, resulting in 6,000 estimates of predicted richness for each patch.size or amount value.

### **Species Distribution Models for Common Breeding Species**

Species distribution models (SDMs) can provide detailed predictions about animal locations, and thus are invaluable to conservation and management efforts (Elith et al. 2006). In recent decades, the availability of remote sensing data has flourished, offering opportunities to develop SDMs over broad geographical ranges (Shirley et al. 2013). For instance, the USGS launched their Landsat 5 satellite in the mid 1980s which takes aerial images of all locations on the earth every 16 days (Kerr & Ostrovsky 2003). With a resolution of 30 m, the resulting data offer opportunities to develop distributional maps over fine temporal and spatial scales.

We used a recently developed approach (Shirley et al. 2013) to model distribution patterns observed from our point count data as a function of Landsat 5 TM imagery information. This allowed us to create SDMs for common breeding bird species across southern Indiana. We began by examining all images taken of our study region in 2011-2013 and eliminated those obscured by clouds or darkness. We then inspected the remaining images, and selected a single image from 29 June 2011 to construct explanatory variables (Figure 1.3). Cloud cover in this image was less than 1 %, and the quality rating for each of the 7 TM bands was excellent. No additional image processing was required given that the single image encompassed our entire study area.

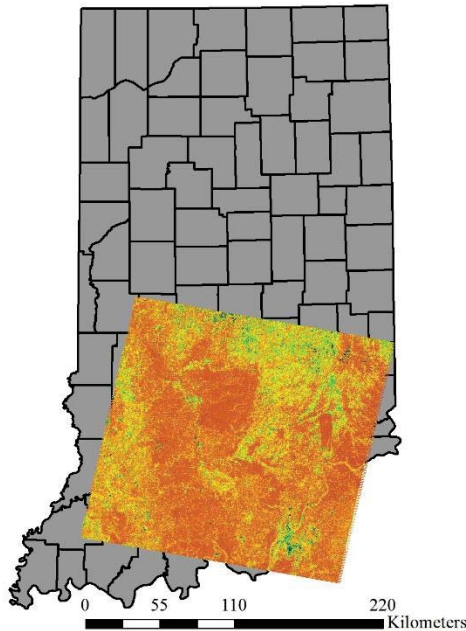
We began by constructing boosted regression tree models (BRTs; Friedman et al. 2000; Friedman 2001) for the 30 most widely distributed species (Table 2). BRTs differ from traditional regression models in that they start with a simple classification tree and use a boosting algorithm to iteratively fit new trees in a stage-wise fashion, where new trees place emphasis on observations thus far poorly predicted (Elith et al. 2008; Shirley et al. 2013). A BRT approach to SD modeling is advantageous because BRTs can construct complex nonlinear relationships and interactions between explanatory variables (Shirley et al. 2013). Further, collinearity among explanatory variables does not pose a problem to BRTs, which do not rely on inversion of matrices like linear models do (Breiman et al. 1984). While the output from BRT analyses is often more challenging to interpret, predictive performance is typically improved.

Explanatory variables in our models were the mean and standard deviation of: the Landsat reflectance bands 1, 2, 3, 4, 5, and 7; elevation, as derived from the USGS National Elevation Dataset (<http://datagateway.nrcs.usda.gov>); and stream distance, derived from the USGS National Hydrography Dataset (<http://datagateway.nrcs.usda.gov>). These values were calculated at 4 spatial scales (150 m, 500 m, 1000 m, and 2000 m) that are known to be relevant to passerines (Betts et al. 2006). Accounting for imperfect detection is currently not possible in a BRT modeling framework, so we also included observer, time of day, and Julian date as explanatory variables for occupancy, resulting in 67 total predictor variables.

We utilized all point count data collected within 100 m of the 654 point count stations sampled in 2011-2013. Each visit (9 total) to each site was used as a unique observation in order to allow inclusion of sample-level covariates (time, observer, and date). Thus, the response variable is effectively the proportion of the visits to a site in which the species was encountered. We randomly split the dataset in half, and information from 327 sites was used for constructing BRTs, while the data from the other sites was used for model validation. Following Elith et al. (2008), we chose a bag fraction (which controls model stochasticity) of 0.5, which typically yield's good results for presence-absence data. The learning rate, which controls the rate at which new trees are added to the model, was set at 0.0025 for all species except for Hairy Woodpecker, for

which learning rate was set to 0.00125. These learning rates resulted in models that achieved the recommended minimum of 1000 trees for each species (Elith et al. 2008). Tree complexity was set to 5, and we used a 10 fold cross-validation procedure in the fitting function (Hastie et al. 2001). All models were fit using the `gbm` (Ridgeway 2015) and `dismo` (Hijmans et al. 2016) packages in R v. 3.2.2.

Fitted models were evaluated with the held out test dataset using the area under the receiver operating characteristic curve (AUC). Hosmer & Lemeshow (2000) suggest that models with an AUC of less than 0.7 do not have acceptable discriminatory power, and thus we only constructed SDMs for those species with a model AUC greater than this value. SDMs were constructed by predicting occupancy at the 30 m pixel level based on the final BRT models to all forested areas covered by the original selected Landsat 5 image (Figure 1.4). We used a constant observer, time, and date for predictions, so the



**Figure 1.4** TM band 1 data from the aerial Landsat 5 image taken on 29 June 2011. The extent indicates the region of coverage for constructed SDMs.

resulting pixel values can be interpreted as the probability that an average observer would observe the species at 6:30 am on June 1.

## Results and Discussion

### Point Counts and Vegetation Sampling

Over the course of 4 years, we conducted 6,639 bird surveys and recorded 109,448 detections of 109 unique species (Table 1.2). Counts of individual species ranged from 0 to as high as 3197 in each year, while naïve occupancy estimates were as high as 0.99 for some species. The majority of these species ( $n = 56$ ) were incidental detections of non-targeted species (*e.g.*, waterbirds, raptors, swifts, swallows, etc.), and were excluded from all analyses. Table 1.2 identifies the particular species that *were* included in each analysis.

We additionally conducted 1,376 vegetation surveys. Each of the 683 sites were sampled twice, and 10 additional points were sampled a third time due to local disturbances. Local vegetation was highly variable among sites (Table 1.3), allowing us to classify species distributions over a broad range of characteristics. Results from the principal components analysis are presented in Table 1.4. As mentioned above, we were not explicitly interested in the effects of local vegetation on species distributions, but rather in accounting for the local variability in our analysis landscape features. This was primarily a tool for reducing the number of explanatory variables in our model, and thus the results are not discussed further.

**Table 1.2** Raw counts and naïve occupancy estimates for all species encountered within 100 m of point count stations during the breeding seasons of 2011-2014. Note that while there were a total of 683 stations, only 654 were sampled in 2011, and 193 in 2014. The latter 3 columns identify which species were utilized in the 3 analyses described in the methods. Species are listed in taxonomic order.

Species	Scientific Name	Raw Counts				Naïve Occupancy				Analyses		
		2011	2012	2013	2014	2011	2012	2013	2014	TE	Dyn Occ	SDM
Canada Goose	<i>Branta canadensis</i>	12	26	2	0	0.008	0.013	0.003	0.000	--	--	--
Wood Duck	<i>Aix sponsa</i>	1	2	0	10	0.002	0.003	0.000	0.016	--	--	--
Mallard	<i>Anas platyrhynchos</i>	2	0	0	0	0.003	0.000	0.000	0.000	--	--	--
Northern Bobwhite	<i>Colinus virginianus</i>	23	40	20	14	0.029	0.044	0.022	0.052	--	--	--
Ruffed Grouse	<i>Bonasa umbellus</i>	0	1	0	0	0.000	0.001	0.000	0.000	--	--	--
Wild Turkey	<i>Meleagris gallopavo</i>	32	39	19	12	0.043	0.020	0.019	0.021	--	--	--
Great Blue Heron	<i>Ardea herodias</i>	12	26	12	0	0.017	0.019	0.016	0.000	--	--	--
Unknown Ardeid	--	0	12	3	0	0.000	0.004	0.003	0.000	--	--	--
Unknown Waterbird	--	1	6	7	0	0.002	0.007	0.010	0.000	--	--	--
Black Vulture	<i>Coragyps atratus</i>	0	0	1	0	0.000	0.000	0.001	0.000	--	--	--
Turkey Vulture	<i>Cathartes aura</i>	9	0	23	0	0.008	0.000	0.003	0.000	--	--	--
Sharp-shinned Hawk	<i>Accipiter striatus</i>	0	1	0	0	0.000	0.001	0.000	0.000	--	--	--
Cooper's Hawk	<i>Accipiter cooperii</i>	1	1	1	0	0.002	0.001	0.001	0.000	--	--	--
Red-shouldered Hawk	<i>Buteo lineatus</i>	19	39	13	18	0.026	0.051	0.019	0.073	--	--	--
Broad-winged Hawk	<i>Buteo platyterus</i>	3	2	1	2	0.005	0.001	0.001	0.010	--	--	--
Red-tailed Hawk	<i>Buteo jamaicensis</i>	8	10	7	3	0.009	0.010	0.010	0.016	--	--	--
Unknown Raptor	--	6	2	4	0	0.009	0.003	0.006	0.000	--	--	--
American Coot	<i>Fulica americana</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Killdeer	<i>Charadrius vociferus</i>	1	5	6	0	0.002	0.007	0.007	0.000	--	--	--
American Woodcock	<i>Scolopax minor</i>	3	6	3	3	0.005	0.006	0.004	0.010	--	--	--
Mourning Dove	<i>Zenaidura macroura</i>	269	192	253	39	0.278	0.195	0.256	0.161	--	--	--
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	457	192	63	142	0.459	0.205	0.078	0.513	--	--	--
Black-billed Cuckoo	<i>Coccyzus erythrophthalmus</i>	3	1	1	0	0.005	0.001	0.001	0.000	--	--	--
Unknown Cuckoo	--	0	0	2	0	0.000	0.000	0.003	0.000	--	--	--
Eastern Screech-Owl	<i>Megascops asio</i>	0	1	4	0	0.000	0.001	0.006	0.000	--	--	--
Great Horned Owl	<i>Bubo virginianus</i>	1	3	0	1	0.002	0.004	0.000	0.005	--	--	--
Barred Owl	<i>Strix varia</i>	7	4	8	1	0.008	0.006	0.009	0.005	--	--	--
Common Nighthawk	<i>Chordeiles minor</i>	0	0	1	0	0.000	0.000	0.001	0.000	--	--	--
Chuck-will's-widow	<i>Caprimulgus carolinensis</i>	0	0	0	1	0.000	0.000	0.000	0.005	--	--	--
Eastern Whip-poor-will	<i>Caprimulgus vociferus</i>	6	8	1	0	0.006	0.009	0.001	0.000	--	--	--
Chimney Swift	<i>Chaetura pelagica</i>	1	1	23	3	0.002	0.001	0.023	0.010	--	--	--
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	22	36	49	19	0.034	0.050	0.067	0.093	--	--	--
Belted Kingfisher	<i>Megaceryle alcyon</i>	3	4	16	1	0.005	0.006	0.022	0.005	--	--	--
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	43	34	25	3	0.050	0.035	0.031	0.016	--	--	--
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	805	1344	685	347	0.633	0.761	0.587	0.731	YES	YES	YES
Downy Woodpecker	<i>Picoides pubescens</i>	524	660	485	354	0.506	0.608	0.493	0.793	YES	YES	YES
Hairy Woodpecker	<i>Picoides villosus</i>	37	241	204	91	0.050	0.283	0.246	0.301	--	YES	YES
Northern Flicker	<i>Colaptes auratus</i>	183	242	252	118	0.231	0.253	0.297	0.409	--	YES	YES
Pileated Woodpecker	<i>Dryocopus pileatus</i>	221	222	160	80	0.255	0.256	0.189	0.306	--	--	--
Unknown Woodpecker	--	343	453	258	118	0.390	0.473	0.313	0.466	--	--	--
Eastern Wood-Pewee	<i>Contopus virens</i>	1409	1428	1543	450	0.809	0.799	0.814	0.839	YES	YES	YES
Acadian Flycatcher	<i>Empidonax virens</i>	2860	3197	3113	1590	0.873	0.906	0.902	0.995	YES	YES	YES
Least Flycatcher	<i>Empidonax minimus</i>	7	0	0	0	0.011	0.000	0.000	0.000	--	--	--
Eastern Phoebe	<i>Sayornis phoebe</i>	32	28	34	18	0.041	0.034	0.038	0.073	--	--	--



Great Crested Flycatcher	<i>Myiarchus crinitus</i>	213	304	269	88	0.242	0.305	0.280	0.285	--	YES	YES
Eastern Kingbird	<i>Tyrannus tyrannus</i>	2	4	10	3	0.002	0.006	0.013	0.010	--	--	--
Unknown Flycatcher	--	5	3	3	0	0.006	0.003	0.003	0.000	--	--	--
White-eyed Vireo	<i>Vireo griseus</i>	343	340	422	147	0.280	0.262	0.290	0.264	--	YES	YES
Yellow-throated Vireo	<i>Vireo flavifrons</i>	243	364	316	149	0.271	0.375	0.348	0.409	YES	YES	YES
Warbling Vireo	<i>Vireo gilvus</i>	18	12	19	0	0.021	0.009	0.018	0.000	--	--	--
Red-eyed Vireo	<i>Vireo olivaceus</i>	2585	2848	2978	1283	0.939	0.946	0.950	0.995	YES	YES	YES
Unknown Vireo	--	0	4	1	1	0.000	0.004	0.001	0.005	--	--	--
Blue Jay	<i>Cyanocitta cristata</i>	443	448	381	134	0.413	0.372	0.351	0.383	--	YES	YES
American Crow	<i>Corvus brachyrhynchos</i>	389	459	241	49	0.355	0.343	0.206	0.145	--	--	--
Purple Martin	<i>Progne subis</i>	0	0	2	0	0.000	0.000	0.001	0.000	--	--	--
Tree Swallow	<i>Tachycineta bicolor</i>	6	0	13	0	0.006	0.000	0.018	0.000	--	--	--
Northern Rough-winged Swallow	<i>Stelgidopteryx serripennis</i>	0	3	1	0	0.000	0.001	0.001	0.000	--	--	--
Barn Swallow	<i>Hirundo rustica</i>	0	1	1	0	0.000	0.001	0.001	0.000	--	--	--
Unknown Swallow	--	0	11	14	0	0.000	0.013	0.013	0.000	--	--	--
Carolina Chickadee	<i>Poecile carolinensis</i>	871	599	872	299	0.607	0.471	0.668	0.653	YES	YES	YES
Tufted Titmouse	<i>Baeolophus bicolor</i>	1673	1470	1553	537	0.872	0.833	0.852	0.907	YES	YES	YES
Unknown Paridae	--	66	222	146	40	0.078	0.240	0.167	0.114	--	--	--
White-breasted Nuthatch	<i>Sitta carolinensis</i>	649	1016	673	533	0.567	0.735	0.605	0.907	YES	YES	YES
Carolina Wren	<i>Thryothorus ludovicianus</i>	622	840	1063	127	0.502	0.615	0.698	0.321	--	YES	YES
House Wren	<i>Troglodytes aedon</i>	3	6	9	0	0.005	0.009	0.012	0.000	--	--	--
Unknown Wren	--	0	0	1	0	0.000	0.000	0.001	0.000	--	--	--
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	1109	719	1245	600	0.769	0.517	0.795	0.933	YES	YES	YES
Eastern Bluebird	<i>Sialia sialis</i>	11	26	50	5	0.015	0.037	0.067	0.026	--	--	--
Veery	<i>Catharus fuscescens</i>	0	1	1	0	0.000	0.001	0.001	0.000	--	--	--
Swainson's Thrush	<i>Catharus ustulatus</i>	0	0	2	0	0.000	0.000	0.003	0.000	--	--	--
Wood Thrush	<i>Hylocichla mustelina</i>	1642	1652	1362	943	0.734	0.710	0.676	0.896	YES	YES	YES
American Robin	<i>Turdus migratorius</i>	252	337	252	34	0.209	0.239	0.218	0.093	--	--	--
Unknown Thrush	--	0	0	1	0	0.000	0.000	0.001	0.000	--	--	--
Gray Catbird	<i>Dumetella carolinensis</i>	200	169	151	63	0.208	0.132	0.136	0.171	--	YES	YES
Northern Mockingbird	<i>Mimus polyglottos</i>	11	1	1	0	0.017	0.001	0.001	0.000	--	--	--
Brown Thrasher	<i>Toxostoma rufum</i>	37	33	29	2	0.047	0.041	0.041	0.005	--	--	--
Unknown Mimic	--	3	1	5	0	0.005	0.001	0.007	0.000	--	--	--
European Starling	<i>Sturnus vulgaris</i>	4	0	1	0	0.003	0.000	0.001	0.000	--	--	--
Cedar Waxwing	<i>Bombicilla cedrorum</i>	5	95	11	9	0.008	0.063	0.010	0.016	--	--	--
Ovenbird	<i>Seiurus aurocapilla</i>	591	650	625	440	0.369	0.404	0.378	0.694	YES	YES	YES
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	114	64	107	101	0.125	0.066	0.111	0.238	--	--	--
Louisiana Waterthrush	<i>Parkesia motacilla</i>	73	88	199	92	0.089	0.110	0.206	0.285	--	--	--
Unknown Waterthrush	--	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	43	21	37	13	0.054	0.023	0.048	0.052	--	--	--
Black-and-white Warbler	<i>Mniotilta varia</i>	21	21	20	25	0.023	0.022	0.026	0.083	--	--	--
Prothonotary Warbler	<i>Protonotaria citrea</i>	94	58	70	23	0.066	0.051	0.057	0.031	--	--	--
Tennessee Warbler	<i>Oreothlypis peregrina</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Nashville Warbler	<i>Oreothlypis ruficapilla</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Kentucky Warbler	<i>Geothlypis formosa</i>	1036	1131	982	446	0.706	0.726	0.690	0.782	YES	YES	YES
Common Yellowthroat	<i>Geothlypis trichas</i>	352	434	354	53	0.303	0.315	0.283	0.135	--	YES	YES
Hooded Warbler	<i>Setophaga citrina</i>	408	377	418	258	0.301	0.256	0.271	0.440	YES	YES	YES
American Redstart	<i>Setophaga ruticilla</i>	12	37	33	30	0.017	0.038	0.040	0.047	--	--	--
Cerulean Warbler	<i>Setophaga cerulea</i>	84	88	116	89	0.098	0.083	0.117	0.228	--	--	--
Northern Parula	<i>Setophaga americana</i>	583	529	625	194	0.468	0.430	0.498	0.440	--	YES	YES
Blackburnian Warbler	<i>Setophaga fusca</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Yellow Warbler	<i>Setophaga petechia</i>	4	4	1	0	0.006	0.004	0.001	0.000	--	--	--
Blackpoll Warbler	<i>Setophaga striata</i>	0	0	1	0	0.000	0.000	0.001	0.000	--	--	--
Pine Warbler	<i>Setophaga pinus</i>	9	2	7	3	0.011	0.003	0.009	0.016	--	--	--
Yellow-rumped Warbler	<i>Setophaga coronata</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Yellow-throated Warbler	<i>Setophaga dominica</i>	226	191	196	43	0.243	0.180	0.204	0.124	--	YES	YES
Prairie Warbler	<i>Setophaga discolor</i>	54	72	71	18	0.063	0.081	0.083	0.052	--	--	--
Black-throated Green Warbler	<i>Setophaga virens</i>	2	3	0	0	0.003	0.003	0.000	0.000	--	--	--
Yellow-breasted Chat	<i>Icteria virens</i>	366	340	274	90	0.295	0.259	0.227	0.212	--	YES	YES
Unknown Warbler	--	8	30	63	9	0.012	0.040	0.078	0.041	--	--	--
Unknown Tanager	--	147	206	84	8	0.176	0.245	0.116	0.041	--	--	--
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	1442	1476	1569	384	0.746	0.712	0.750	0.653	YES	YES	YES
Chipping Sparrow	<i>Spizella passerina</i>	54	12	43	4	0.072	0.018	0.048	0.021	--	--	--
Field Sparrow	<i>Spizella pusilla</i>	131	82	149	16	0.142	0.089	0.142	0.041	--	--	--
Song Sparrow	<i>Melospiza melodia</i>	59	69	108	3	0.067	0.064	0.107	0.010	--	--	--
Summer Tanager	<i>Piranga rubra</i>	257	216	212	66	0.295	0.237	0.236	0.233	--	YES	YES
Scarlet Tanager	<i>Piranga olivacea</i>	673	700	768	455	0.592	0.593	0.592	0.839	YES	YES	YES
Northern Cardinal	<i>Cardinalis cardinalis</i>	2013	1995	1942	391	0.873	0.827	0.848	0.715	YES	YES	YES
Rose-breasted Grosbeak	<i>Phaeucticus ludovicianus</i>	7	13	17	20	0.011	0.013	0.016	0.047	--	--	--

Blue Grosbeak	<i>Passerina caerulea</i>	0	0	1	0	0.000	0.000	0.001	0.000	--	--	--
Indigo Bunting	<i>Passerina cyanea</i>	1410	1546	1277	221	0.742	0.725	0.695	0.492	YES	YES	YES
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	42	35	33	1	0.031	0.029	0.029	0.005	--	--	--
Eastern Meadowlark	<i>Sturnella magna</i>	3	2	2	0	0.003	0.003	0.001	0.000	--	--	--
Common Grackle	<i>Quiscalus quiscula</i>	47	37	17	0	0.031	0.022	0.012	0.000	--	--	--
Brown-headed Cowbird	<i>Molothrus ater</i>	1216	1220	1041	686	0.783	0.772	0.738	0.943	YES	--	--
Orchard Oriole	<i>Icterus spurius</i>	2	4	4	0	0.003	0.004	0.006	0.000	--	--	--
Baltimore Oriole	<i>Icterus galbula</i>	47	24	25	4	0.060	0.035	0.032	0.021	--	--	--
Unknown Icterid	--	14	25	12	0	0.009	0.018	0.018	0.000	--	--	--
House Finch	<i>Carpodacus mexicanus</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
American Goldfinch	<i>Spinus tristis</i>	88	147	136	48	0.115	0.160	0.152	0.140	--	--	--
House Sparrow	<i>Passer domesticus</i>	1	0	0	0	0.002	0.000	0.000	0.000	--	--	--
Unknown Passerine	--	0	21	177	0	0.000	0.028	0.187	0.000	--	--	--
Unknown Bird	--	538	1361	423	213	0.459	0.820	0.438	0.544	--	--	--

**Table 1.3** Summary of vegetation local and landscape level habitat features at 683 point count stations.

Measured habitat features	Minimum	Maximum	Median	Mean
Edge distance (m)	20.32	659.40	76.08	127.50
% habitat amount	11.22	99.81	63.51	64.28
Patch size (ha)	0.89	22800.00	12.02	405.10
Tree basal area (m <sup>2</sup> /ha)	2.00	52.00	26.00	25.97
% canopy cover	5.00	100.00	90.00	87.39
% shrub cover	0.00	92.50	22.50	26.10
Leaf litter depth (cm)	0.00	7.44	1.88	1.96
Vertical foliage density (proportion contacted)	0.00	0.27	0.09	0.09

**Table 1.4.** Results of the principal components analysis for local vegetation metrics. Condensing the data from local vegetation surveys into principal components allowed us to reduce the number of explanatory variables included in our models while still accounting for a large amount of local variability.

Variable	PC1	PC2	PC3	PC4	PC5
<b>Loadings</b>					
Tree basal area	-0.39	-0.45	0.44	-0.65	0.16
% shrub cover	0.57	-0.39	0.08	-0.19	-0.69
% canopy cover	-0.43	-0.45	0.28	0.69	-0.26
Vertical foliage density	0.55	-0.44	0.15	0.24	0.66
Leaf litter depth	-0.19	-0.50	-0.84	-0.08	0.05
<b>Summary</b>					
Standard deviation	1.34	1.08	0.95	0.85	0.65
Proportion of variance	0.36	0.23	0.18	0.14	0.08
Cumulative variance	0.36	0.59	0.77	0.92	1.00

## Effects of Temporary Emigration on Estimates of Population Dynamics

*Simulated Data-* In the use and super-population sampling scenarios, site closure tests performed very well. In cases where population dynamics did not occur, the static occupancy and abundance models were appropriately selected  $\geq 95.1\%$  and  $\geq 91.9\%$  of the time, respectively, and when population dynamics were present, the dynamic occupancy or abundance model was selected  $\geq 97.2\%$  of the time (Tables 1.5 and 1.6). As expected, in all cases, the estimates of initial distributions approximated  $\psi_0$  or  $\lambda_0$ , while detection estimates approximated  $p_d p_d$ . Accordingly, dynamic parameter estimates were highly accurate and precise estimates of the dynamic population rates.

When secondary sampling periods were closed to TE (occupancy and abundance scenarios), site closure tests and dynamic parameter estimates resulted in misleading conclusions about population dynamics. Where population dynamics were absent, the closed models were appropriately selected  $\leq 1.3\%$  of the time, and when population dynamics were present, the dynamic model was selected 100% of the time (Tables 1.7 and 1.8). As expected, initial distributions estimated from these models tended to approximate  $\psi$  or  $\lambda$  while the detection estimate approximated  $p_d$ . However, the dynamic occupancy models tended to underestimate colonization rates and overestimate extinction rates while dynamic abundance models tended to overestimate recruitment rate and underestimate apparent survival.

*Empirical Case Study-* The results from the analysis of our confounded TE/dynamics and isolated TE datasets were very similar. We found evidence for population dynamics in occupancy and abundance for all 19 species using both datasets ( $P < 0.02$ ; Table 1.9). That is, the dynamic population models had greater support for all species even when the interval between primary sampling periods was limited to 24-48 hours. Estimates of extinction from dynamic occupancy models fit to the confounded TE/dynamics datasets were significantly greater than the estimates from models fit to the isolated TE datasets (Fig. 1.4). However, there was no evidence that estimates of detection, initial occupancy, or colonization differed between these models. Similarly, there was no evidence that estimates of detection, initial abundance, recruitment, or apparent survival differed between dynamic abundance models fit to the confounded TE/dynamics and isolated TE datasets (Fig. 1.4). Therefore, in most cases, the parameter estimates generated by dynamic models were statistically indistinguishable when primary periods were separated by two days versus 17 days. This suggests that the dynamic parameter estimates were heavily influenced by TE when secondary samples occur within 10 minutes of one another.

In contrast, we only found evidence for violations of the closure assumption for nine species using the isolated dynamics presence/absence datasets, and eight species using the isolated dynamics count datasets (Table 9). That is, for most species there was no evidence for population dynamics over the  $\sim 17$  day period when TE was estimated as a component of detection. In presence/absence models, we found strong evidence that estimates of detection and extinction were greater, while initial occupancy was lower in models fit to the confounded TE/dynamics datasets than when fit to the isolated dynamics datasets (Fig. 5). There was also evidence that detection was greater and initial abundance and apparent survival were lower in models fit to confounded TE/dynamics count datasets. These results indicate that models fit to the isolated dynamics datasets are quantifying changes in use or super-population size while models fit to the other datasets are likely measuring changes in instantaneous occupancy or abundance.

Concern about overestimating species distributions due to violations of the closure assumption associated with repeated sampling has led to widespread recommendations that

samples be conducted extremely close together in time (MacKenzie & Royle 2005; MacKenzie 2005; Rota *et al.* 2009; Kendall *et al.* 2013). This allows for instantaneous estimates of density or occupancy, providing valuable information to managers regarding the number of individuals or territories in a study area. However, our simulation results demonstrate that model extensions which allow for quantifying changes in distributions (*e.g.*, MacKenzie *et al.* 2003; Dail & Madsen 2011) confound estimates of TE with population dynamics under such study designs. This does not invalidate estimates of dynamic rates between instantaneous distributions. However, our findings show that these dynamics are the result of two distinctly different processes (TE and population dynamics), and naiveté to this fact could mislead biological interpretations of dynamic rates (*i.e.*, that sites have truly experienced local extinctions rather than become temporarily unoccupied).

Results from our empirical data analysis provide an example of the degree to which this problem could emerge in observational studies. Conducting secondary samples within minutes of one another has become a popular avian sampling technique in recent years (*e.g.*, Betts *et al.* 2008; Rota *et al.* 2009; McClure & Hill 2012; Otto & Roloff 2012). By varying the temporal duration between primary and secondary periods with empirical data, we demonstrated that estimates of population dynamics under this protocol are likely heavily influenced by TE. Nevertheless, numerous studies using this approach have concluded that the dynamic rates modeled between repeated site visits are indicative of within-season dispersal for breeding birds (*e.g.*, Betts *et al.* 2008; Rota *et al.* 2009; McClure & Hill 2012; Otto & Roloff 2012). Indeed, Rota *et al.* (2009) provided a thorough consideration of the influence that TE might have on their results, yet concluded that TE was more than likely not the process being modeled between their 10 minute primary sampling periods. However, using the same sampling protocol, we definitively demonstrated that TE heavily influences estimates of population dynamics, and indeed may be the only process being modeled between primary periods for some species.

Identifying source and sink habitats, or colonization and extinction events on military lands relies on an implicit assumption that the dynamic processes being estimated are indicative of permanent distributional shifts rather than temporary changes in sampling availability. Further, when estimating population trends, confounding between TE and true dynamics can reduce precision of abundance estimates such that longer time periods would be required to detect those trends (Schmidt *et al.* 2013). In each of these cases, TE is a nuisance parameter more appropriately estimated separately from, or as a component of, detection probability. At present, we are unaware of any modeling approaches that simultaneously estimate  $p_a$ ,  $p_d$ , and population dynamics uniquely. Indeed, this would require a third level of information (*e.g.*, tertiary sampling periods). However, as we and others (*e.g.*, Kendall 1999; Schmidt *et al.* 2013) have demonstrated, it is unnecessary to collect such additional information when TE is not of direct interest, because dynamic parameters can be isolated with an appropriate sampling design.

While numerous other methods have been developed to quantify dynamic rates from surveys of unmarked animals, only Pollock's (1982) robust sampling design provides the flexibility for separating temporary and permanent changes in distribution. For instance, the Dail & Madsen (2011, 2013) dynamic distribution models do not require secondary sampling periods, and indeed the authors explicitly define "open" populations as those experiencing changes in site super-population size. However, without repeated visits, detection probability cannot be estimated as  $p_{apd}$  (Nichols *et al.* 2009). Therefore, unless  $p_a$  is equal to one, dynamic rates estimated between single survey visits will always represent changes in instantaneous abundance. Similarly, Sollmann *et al.* (2015) developed a model for estimating dynamics between single-visit surveys

while quantifying detection probability from distance data. Again, because distance-based sampling methods estimate site abundances as  $\lambda op_a$ , one cannot distinguish between permanent distributional shifts and temporary changes in availability.

Modeling population dynamics in the presence of TE therefore requires both repeated samples and nuanced consideration of the spatial and temporal scales over which availability and distributions change. When population dynamics are of interest, researchers and managers should purposefully design studies to estimate use or super-population size within primary periods, rather than instantaneous occupancy or abundance. This requires estimating detection probability as  $pap_d$ , and therefore that the probability of one or more individuals being available for sampling is random and independent during each secondary period (MacKenzie 2005; Nichols et al. 2009). In cases where there is a spatial mismatch between the size of sample sites and the space used by targeted individuals (e.g., Fig. 1.1), this means allowing ample time for spatial redistribution of individuals such that their locations during two sampling events are uncorrelated (Fig. 5). Spatial autocorrelation in locations should decrease with time, but the length of time required to achieve statistical independence will be longer for slower moving species (Swihart & Slade 1985). When the sampling technique itself is destructive or induces a “trap response” (e.g., Otto et al. 2013), the duration between repeated samples may need to be further extended in order to ensure that the availability of individuals on one sampling occasion is not negatively influenced by a previous sampling event. Indeed, in all situations, increasing the amount of time between samples should reduce correlation in availability (e.g., the likelihood that an animal is vocalizing, or has retreated below ground or water), yet critically, the total time interval within a primary sampling period must be sufficiently short that changes in use or super-population sizes are negligible. Otherwise, this process will also be estimated as a component of detection probability (Kendall 1999; Rota et al. 2009).

These recommendations rely on a study system in which TE occurs over a finer time scale than population dynamics, and that the two are sufficiently distinguishable (Fig. 1.6). Designing an appropriate sampling scheme thus requires substantial knowledge about the study system. In our empirical study of territorial breeding birds, we assumed that 24-48 hour periods were long enough to ensure independence among individual bird locations within territories, yet short enough that dynamic rates were negligible. Although we did not evaluate this assumption in the field, a two-day period should allow ample movement for highly vagile species like birds, while substantial changes in site use are unlikely. In other sampling scenarios, however, these processes may not be uniquely identifiable, even with a robust sampling design. For instance, Kendall et al. (1997) noted that non-nesting birds could be considered temporary emigrants when sampling techniques focus on nesting individuals (e.g., Spendelov & Nichols 1989). However, the temporal scale of mating and nest-building may not be distinguishable from that of changes in population size or distributions. Similarly, for species with poorly defined territories or home ranges, TE and dynamics may not be biologically distinct processes. Future work should focus on identifying appropriate temporal sampling scales for different combinations of species and sampling techniques in order to separate rates of dynamics and TE.

**Table 1.5** Results from occupancy models fit to simulated datasets designed to mimic a sampling scheme that tests for and quantifies changes in site use, rather than instantaneous occupancy. We generated 1000 datasets for each combination of simulation parameters. Whether or not any individual using the site was available to be detected was independent during each sampling period, and thus the detection estimates tend to approximate  $p_{apd}$  while the distribution parameters approximate the rate of site use ( $\psi_0$ ). When no changes in site use occurred (no dynamics), static models were chosen the majority of the time. When population dynamics were present, open models were selected most frequently, generating accurate and precise estimates of changes in site use.

Simulation parameters					% open selected	Dist ( $\psi_0$ )		Det ( $p_{apd}$ )		Colonization ( $\gamma$ )				Extinction ( $\epsilon$ )			
$\psi_0$	$p_a$	$p_d$	$\gamma$	$\epsilon$		Mean	Var	Mean	Var	Mean	Var	Bias	MSE	Mean	Var	Bias	MSE
No dynamics																	
0.3	0.5	0.5	0.00	0	3.9	0.30	0.00	0.25	0.00	---	---	---	---	---	---	---	---
0.3	0.5	0.8	0.00	0	4.1	0.30	0.00	0.40	0.00	---	---	---	---	---	---	---	---
0.3	0.8	0.5	0.00	0	4.9	0.30	0.00	0.40	0.00	---	---	---	---	---	---	---	---
0.3	0.8	0.8	0.00	0	3.3	0.30	0.00	0.64	0.00	---	---	---	---	---	---	---	---
0.7	0.5	0.5	0.00	0	3.8	0.70	0.00	0.25	0.00	---	---	---	---	---	---	---	---
0.7	0.5	0.8	0.00	0	4.2	0.70	0.00	0.40	0.00	---	---	---	---	---	---	---	---
0.7	0.8	0.5	0.00	0	4.7	0.70	0.00	0.40	0.00	---	---	---	---	---	---	---	---
0.7	0.8	0.8	0.00	0	3.7	0.70	0.00	0.64	0.00	---	---	---	---	---	---	---	---
Dynamics																	
0.3	0.5	0.5	0.09	0.2	97.2	0.30	0.00	0.25	0.00	0.08	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.5	0.5	0.17	0.4	100	0.32	0.01	0.25	0.00	0.17	0.00	0.00	0.00	0.39	0.01	-0.01	0.01
0.3	0.5	0.8	0.09	0.2	100	0.30	0.00	0.40	0.00	0.08	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.5	0.8	0.17	0.4	100	0.30	0.00	0.40	0.00	0.17	0.00	0.00	0.00	0.40	0.00	0.00	0.00
0.3	0.8	0.5	0.09	0.2	100	0.30	0.00	0.40	0.00	0.09	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.8	0.5	0.17	0.4	100	0.30	0.00	0.40	0.00	0.17	0.00	0.00	0.00	0.40	0.00	0.00	0.00
0.3	0.8	0.8	0.09	0.2	100	0.30	0.00	0.64	0.00	0.09	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.3	0.8	0.8	0.17	0.4	100	0.30	0.00	0.64	0.00	0.17	0.00	0.00	0.00	0.40	0.00	0.00	0.00
0.7	0.5	0.5	0.47	0.2	100*	0.70	0.00	0.25	0.00	0.45	0.01	-0.01	0.01	0.20	0.00	0.00	0.00
0.7	0.5	0.5	0.93	0.4	100†	0.70	0.00	0.25	0.00	0.92	0.01	-0.01	0.01	0.40	0.00	0.00	0.00
0.7	0.5	0.8	0.47	0.2	100	0.70	0.00	0.40	0.00	0.47	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.7	0.5	0.8	0.93	0.4	100	0.70	0.00	0.40	0.00	0.94	0.00	0.01	0.00	0.40	0.00	0.00	0.00
0.7	0.8	0.5	0.47	0.2	100	0.70	0.00	0.40	0.00	0.47	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.7	0.8	0.5	0.93	0.4	100	0.70	0.00	0.40	0.00	0.95	0.00	0.01	0.00	0.40	0.00	0.00	0.00
0.7	0.8	0.8	0.47	0.2	100	0.70	0.00	0.64	0.00	0.47	0.00	0.00	0.00	0.20	0.00	0.00	0.00
0.7	0.8	0.8	0.93	0.4	100	0.70	0.00	0.64	0.00	0.93	0.00	0.00	0.00	0.40	0.00	0.00	0.00

Percentages for \* and † are based on 997 and 936 comparisons, respectively, because closed models could not be fit to some datasets.



**Table 1.6** Results from abundance models fit to simulated datasets designed to mimic a sampling scheme that tests for and quantifies changes in site superpopulation size, rather than instantaneous abundance. We generated 1000 datasets for each combination of simulation parameters. Whether or not each individual using the site was available to be detected was independent during each sampling period, and thus the detection estimates tend to approximate  $p_{apd}$  while the distribution parameters approximate the superpopulation size ( $\lambda_0$ ). When no changes in site superpopulation occurred (no dynamics), static models were chosen the majority of the time. When population dynamics were present, open models were selected most frequently, generating accurate and precise estimates of changes in superpopulation size.

Simulation parameters					% open selected	Dist ( $\lambda_0$ )		Det ( $p_{apd}$ )		Recruitment ( $\phi$ )				Apparent survival ( $\omega$ )			
$\lambda_0$	$p_a$	$p_d$	$\phi$	$\omega$		Mean	Var	Mean	Var	Mean	Var	Bias	MSE	Mean	Var	Bias	MSE
No dynamics																	
1.0	0.5	0.5	0.0	1.0	7.8	1.00	0.00	0.25	0.00	---	---	---	---	---	---	---	---
1.0	0.5	0.8	0.0	1.0	5.3	1.00	0.00	0.40	0.00	---	---	---	---	---	---	---	---
1.0	0.8	0.5	0.0	1.0	5.5	1.00	0.00	0.40	0.00	---	---	---	---	---	---	---	---
1.0	0.8	0.8	0.0	1.0	4.5	1.00	0.00	0.64	0.00	---	---	---	---	---	---	---	---
2.0	0.5	0.5	0.0	1.0	8.1	2.01	0.01	0.25	0.00	---	---	---	---	---	---	---	---
2.0	0.5	0.8	0.0	1.0	5.8	2.00	0.01	0.40	0.00	---	---	---	---	---	---	---	---
2.0	0.8	0.5	0.0	1.0	7.6	2.00	0.01	0.40	0.00	---	---	---	---	---	---	---	---
2.0	0.8	0.8	0.0	1.0	3.3	2.00	0.00	0.64	0.00	---	---	---	---	---	---	---	---
Dynamics																	
1.0	0.5	0.5	0.2	0.8	100	1.00	0.01	0.25	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
1.0	0.5	0.5	0.4	0.6	100	1.01	0.01	0.25	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00
1.0	0.5	0.8	0.2	0.8	100	1.00	0.00	0.40	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
1.0	0.5	0.8	0.4	0.6	100	1.00	0.00	0.40	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00
1.0	0.8	0.5	0.2	0.8	100	1.00	0.00	0.40	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
1.0	0.8	0.5	0.4	0.6	100	1.00	0.00	0.40	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00
1.0	0.8	0.8	0.2	0.8	100	1.00	0.00	0.64	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
1.0	0.8	0.8	0.4	0.6	100	1.00	0.00	0.64	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00
2.0	0.5	0.5	0.2	0.8	100	2.02	0.02	0.25	0.00	0.20	0.01	0.00	0.01	0.80	0.00	0.00	0.00
2.0	0.5	0.5	0.4	0.6	100	2.02	0.02	0.25	0.00	0.40	0.01	0.00	0.01	0.60	0.00	0.00	0.00
2.0	0.5	0.8	0.2	0.8	100	2.01	0.01	0.40	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
2.0	0.5	0.8	0.4	0.6	100	2.00	0.01	0.40	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00
2.0	0.8	0.5	0.2	0.8	100	2.01	0.01	0.40	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
2.0	0.8	0.5	0.4	0.6	100	2.00	0.01	0.40	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00
2.0	0.8	0.8	0.2	0.8	100	2.00	0.01	0.64	0.00	0.20	0.00	0.00	0.00	0.80	0.00	0.00	0.00
2.0	0.8	0.8	0.4	0.6	100	2.00	0.00	0.64	0.00	0.40	0.00	0.00	0.00	0.60	0.00	0.00	0.00

**Table 1.7** Results from occupancy models fit to simulated datasets designed to mimic a sampling scheme that tests for and quantifies changes in instantaneous occupancy, rather than site use. We generated 1000 datasets for each combination of simulation parameters. Whether or not any individual using the site was available to be detected could only change every third visit between primary periods, and thus the detection estimates tend to approximate  $p_d$  while the distribution parameters approximate the instantaneous occupancy rate ( $\psi_0 p_a$ ). Dynamic models were selected nearly 100% of the time regardless of whether changes in site use actually occurred. Consequently, the colonization and extinction rates are overestimate those rates of change because they are confounded with changes in instantaneous occupancy stemming from temporary emigration.

Simulation parameters					% open selected	Dist ( $\psi_0 p_a$ )		Det ( $p_d$ )		Colonization ( $\gamma$ )				Extinction ( $\epsilon$ )			
$\psi_0$	$p_a$	$p_d$	$\gamma$	$\epsilon$		Mean	Var	Mean	Var	Mean	Var	Bias	MSE	Mean	Var	Bias	MSE
No dynamics																	
0.3	0.5	0.5	0.00	0	100	0.16	0.00	0.47	0.00	0.07	0.00	0.07	0.01	0.39	0.00	0.39	0.15
0.3	0.5	0.8	0.00	0	100	0.15	0.00	0.80	0.00	0.09	0.00	0.09	0.01	0.49	0.00	0.49	0.24
0.3	0.8	0.5	0.00	0	98.7	0.26	0.00	0.46	0.00	0.03	0.00	0.03	0.00	0.08	0.00	0.08	0.01
0.3	0.8	0.8	0.00	0	99.9	0.24	0.00	0.78	0.00	0.05	0.00	0.05	0.00	0.15	0.00	0.15	0.02
0.7	0.5	0.5	0.00	0	100	0.35	0.00	0.50	0.00	0.26	0.00	0.26	0.07	0.48	0.00	0.48	0.24
0.7	0.5	0.8	0.00	0	100	0.35	0.00	0.80	0.00	0.27	0.00	0.27	0.07	0.50	0.00	0.50	0.25
0.7	0.8	0.5	0.00	0	99.6	0.58	0.00	0.47	0.00	0.17	0.00	0.17	0.03	0.11	0.00	0.11	0.01
0.7	0.8	0.8	0.00	0	100	0.56	0.00	0.80	0.00	0.25	0.00	0.25	0.06	0.19	0.00	0.19	0.04
Dynamics																	
0.3	0.5	0.5	0.09	0.2	100	0.15	0.00	0.49	0.00	0.10	0.00	0.02	0.00	0.57	0.00	0.37	0.14
0.3	0.5	0.5	0.17	0.4	100	0.15	0.00	0.50	0.00	0.12	0.00	-0.05	0.00	0.70	0.00	0.30	0.09
0.3	0.5	0.8	0.09	0.2	100	0.15	0.00	0.80	0.00	0.11	0.00	0.02	0.00	0.60	0.00	0.40	0.16
0.3	0.5	0.8	0.17	0.4	100	0.15	0.00	0.80	0.00	0.12	0.00	-0.05	0.00	0.70	0.00	0.30	0.09
0.3	0.8	0.5	0.09	0.2	100	0.24	0.00	0.49	0.00	0.10	0.00	0.02	0.00	0.32	0.00	0.12	0.02
0.3	0.8	0.5	0.17	0.4	100	0.24	0.00	0.50	0.00	0.16	0.00	-0.01	0.00	0.52	0.00	0.12	0.01
0.3	0.8	0.8	0.09	0.2	100	0.24	0.00	0.80	0.00	0.11	0.00	0.03	0.00	0.36	0.00	0.16	0.03
0.3	0.8	0.8	0.17	0.4	100	0.24	0.00	0.80	0.00	0.16	0.00	-0.01	0.00	0.52	0.00	0.12	0.02
0.7	0.5	0.5	0.47	0.2	100	0.35	0.00	0.50	0.00	0.32	0.00	-0.14	0.02	0.60	0.00	0.40	0.16
0.7	0.5	0.5	0.93	0.4	100	0.35	0.00	0.50	0.00	0.38	0.00	-0.55	0.31	0.70	0.00	0.30	0.09
0.7	0.5	0.8	0.47	0.2	100	0.35	0.00	0.80	0.00	0.32	0.00	-0.14	0.02	0.60	0.00	0.40	0.16
0.7	0.5	0.8	0.93	0.4	100	0.35	0.00	0.80	0.00	0.38	0.00	-0.56	0.31	0.70	0.00	0.30	0.09
0.7	0.8	0.5	0.47	0.2	100	0.56	0.00	0.50	0.00	0.46	0.00	-0.01	0.00	0.36	0.00	0.16	0.03
0.7	0.8	0.5	0.93	0.4	100	0.56	0.00	0.50	0.00	0.66	0.00	-0.27	0.07	0.52	0.00	0.12	0.02
0.7	0.8	0.8	0.47	0.2	100	0.56	0.00	0.80	0.00	0.46	0.00	-0.01	0.00	0.36	0.00	0.16	0.03
0.7	0.8	0.8	0.93	0.4	100	0.56	0.00	0.80	0.00	0.66	0.00	-0.27	0.07	0.52	0.00	0.12	0.02

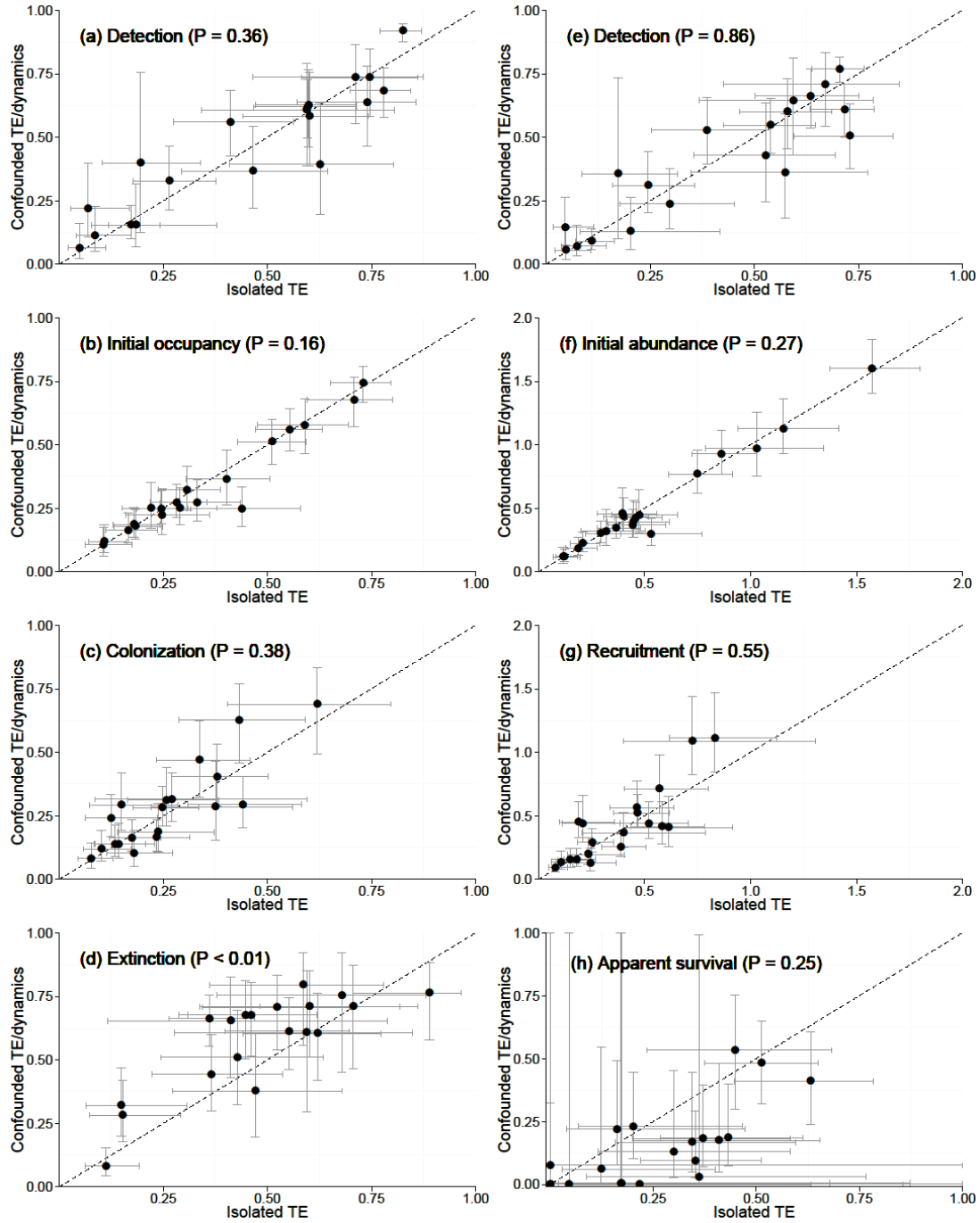


**Table 1.8** Results from abundance models fit to simulated datasets designed to mimic a sampling scheme that tests for and quantifies changes in instantaneous abundance, rather than superpopulation size. We generated 1000 datasets for each combination of simulation parameters. Whether or not each individual using the site was available to be detected could only change every third visit between primary periods, and thus the detection estimates tend to approximate  $p_d$  while the distribution parameters approximate instantaneous abundance ( $\lambda_0 p_a$ ). Dynamic models were selected nearly 100% of the time regardless of whether changes in superpopulation size actually occurred. Consequently, the estimates of recruitment and apparent survival are biased for those rates of change because they are confounded with changes in instantaneous abundance stemming from temporary emigration.

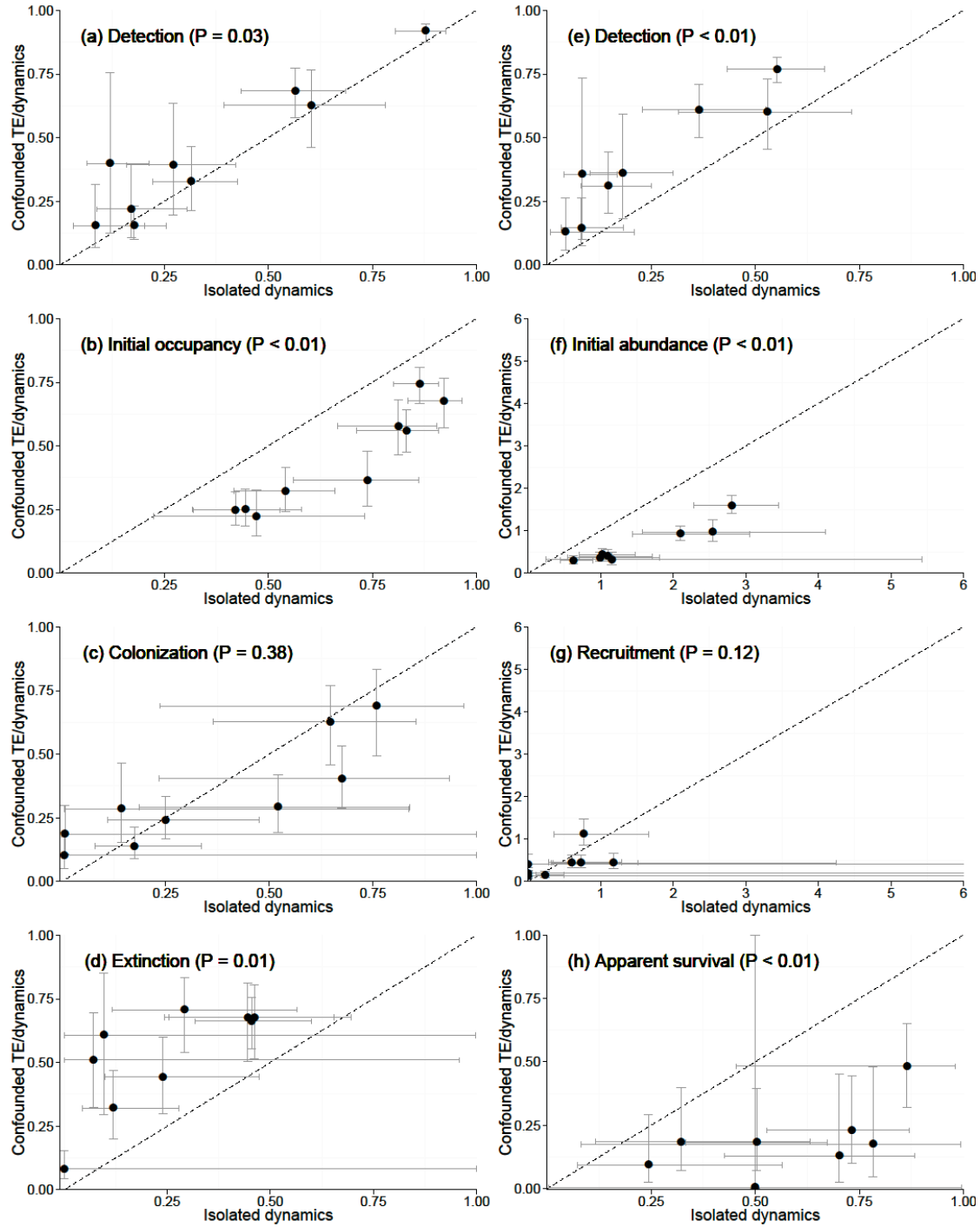
Simulation parameters					% open selected	Dist ( $\lambda_0 p_a$ )		Det ( $p_d$ )		Recruitment ( $\phi$ )				Apparent survival ( $\omega$ )			
$\lambda_0$	$p_a$	$p_d$	$\phi$	$\omega$		Mean	Var	Mean	Var	Mean	Var	Bias	MSE	Mean	Var	Bias	MSE
No dynamics																	
1.0	0.5	0.5	0.0	1.0	100	0.51	0.00	0.48	0.00	0.22	0.00	0.22	0.05	0.57	0.00	-0.43	0.19
1.0	0.5	0.8	0.0	1.0	100	0.50	0.00	0.80	0.00	0.25	0.00	0.25	0.06	0.50	0.00	-0.50	0.25
1.0	0.8	0.5	0.0	1.0	100	0.85	0.00	0.47	0.00	0.08	0.00	0.08	0.01	0.90	0.00	-0.10	0.01
1.0	0.8	0.8	0.0	1.0	100	0.80	0.00	0.79	0.00	0.14	0.00	0.14	0.02	0.83	0.00	-0.17	0.03
2.0	0.5	0.5	0.0	1.0	100	1.01	0.00	0.49	0.00	0.46	0.00	0.46	0.22	0.55	0.00	-0.45	0.21
2.0	0.5	0.8	0.0	1.0	100	1.00	0.00	0.80	0.00	0.50	0.00	0.50	0.25	0.50	0.00	-0.50	0.25
2.0	0.8	0.5	0.0	1.0	98.9	1.68	0.01	0.48	0.00	0.19	0.00	0.19	0.04	0.89	0.00	-0.11	0.01
2.0	0.8	0.8	0.0	1.0	100	1.61	0.00	0.79	0.00	0.29	0.00	0.29	0.08	0.82	0.00	-0.18	0.03
Dynamics																	
1.0	0.5	0.5	0.2	0.8	100	0.50	0.00	0.49	0.00	0.29	0.00	0.09	0.01	0.42	0.00	-0.38	0.14
1.0	0.5	0.5	0.4	0.6	100	0.50	0.00	0.50	0.00	0.35	0.00	-0.05	0.00	0.31	0.00	-0.29	0.09
1.0	0.5	0.8	0.2	0.8	100	0.50	0.00	0.80	0.00	0.30	0.00	0.10	0.01	0.40	0.00	-0.40	0.16
1.0	0.5	0.8	0.4	0.6	100	0.50	0.00	0.80	0.00	0.35	0.00	-0.05	0.00	0.30	0.00	-0.30	0.09
1.0	0.8	0.5	0.2	0.8	100	0.81	0.00	0.49	0.00	0.27	0.00	0.07	0.01	0.67	0.00	-0.13	0.02
1.0	0.8	0.5	0.4	0.6	100	0.80	0.00	0.50	0.00	0.41	0.00	0.01	0.00	0.49	0.00	-0.11	0.01
1.0	0.8	0.8	0.2	0.8	100	0.80	0.00	0.80	0.00	0.29	0.00	0.09	0.01	0.64	0.00	-0.16	0.02
1.0	0.8	0.8	0.4	0.6	100	0.80	0.00	0.80	0.00	0.42	0.00	0.02	0.00	0.48	0.00	-0.12	0.01
2.0	0.5	0.5	0.2	0.8	100	1.01	0.00	0.50	0.00	0.46	0.00	0.26	0.07	0.42	0.00	-0.38	0.15
2.0	0.5	0.5	0.4	0.6	100	1.01	0.00	0.50	0.00	0.46	0.00	0.06	0.00	0.31	0.00	-0.29	0.08
2.0	0.5	0.8	0.2	0.8	100	1.00	0.00	0.80	0.00	0.48	0.00	0.28	0.08	0.40	0.00	-0.40	0.16
2.0	0.5	0.8	0.4	0.6	100	1.00	0.00	0.80	0.00	0.47	0.00	0.07	0.01	0.30	0.00	-0.30	0.09
2.0	0.8	0.5	0.2	0.8	100	1.62	0.00	0.49	0.00	0.36	0.00	0.16	0.03	0.67	0.00	-0.13	0.02
2.0	0.8	0.5	0.4	0.6	100	1.61	0.01	0.50	0.00	0.48	0.00	0.08	0.01	0.49	0.00	-0.11	0.01
2.0	0.8	0.8	0.2	0.8	100	1.60	0.00	0.80	0.00	0.40	0.00	0.20	0.04	0.65	0.00	-0.15	0.02
2.0	0.8	0.8	0.4	0.6	100	1.60	0.00	0.80	0.00	0.49	0.00	0.09	0.01	0.48	0.00	-0.12	0.01

**Table 1.9** The 19 species for which site closure was evaluated under 3 different sampling scenarios (confounded TE/dynamics, isolated TE, and isolated dynamics). The data were based on repeated visits to 193 point count locations in southern Indiana in the summer of 2014.

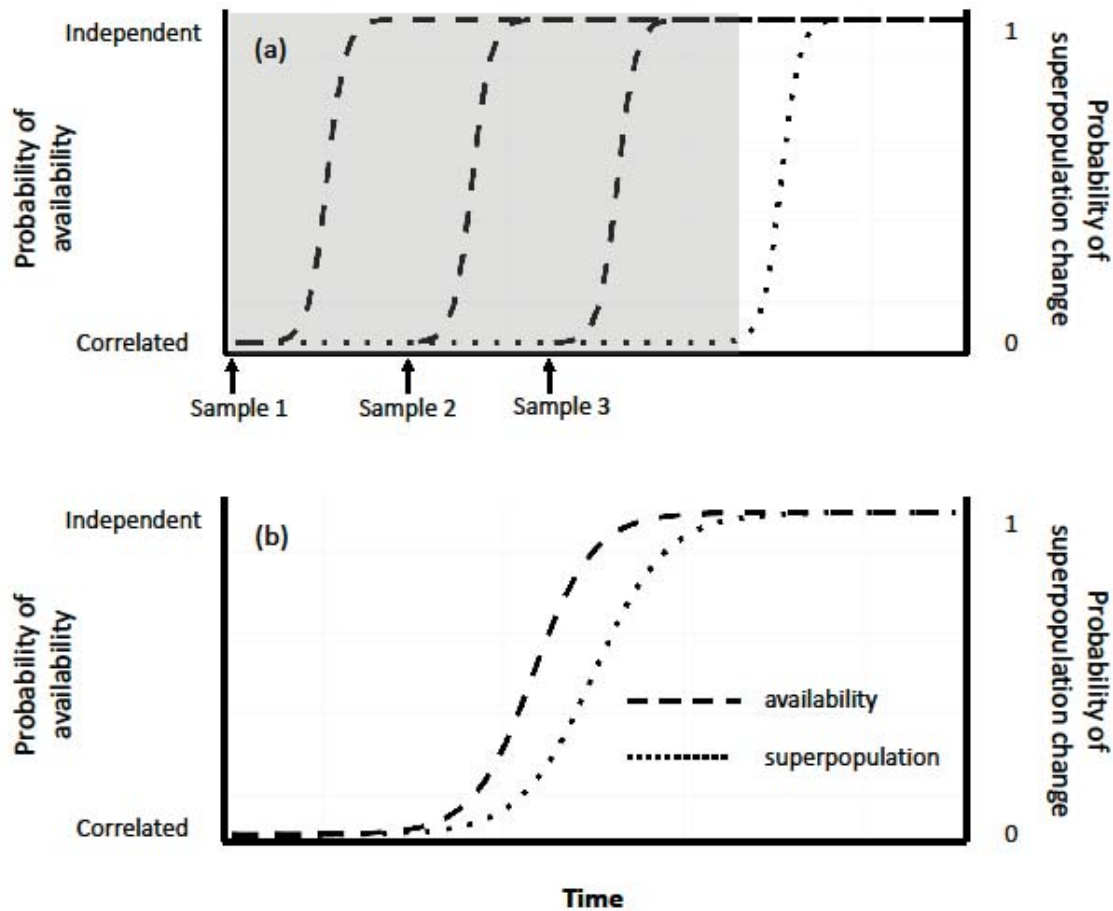
Species	Scientific name	Naïve occupancy	Occ. closure test p-values		Naïve mean site abundance	Abund. closure test p-values	
			TE	dynamics		TE	dynamics
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	0.37	< 0.001	0.006	0.45	< 0.001	0.02
Downy Woodpecker	<i>Picoides pubescens</i>	0.53	< 0.001	< 0.001	0.68	< 0.001	0.20
Eastern Wood-Pewee	<i>Contopus virens</i>	0.44	< 0.001	0.01	0.52	< 0.001	0.16
Acadian Flycatcher	<i>Empidonax virescens</i>	0.92	< 0.001	< 0.001	2.15	< 0.001	0.002
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0.25	< 0.001	< 0.001	0.26	< 0.001	0.31
Red-eyed Vireo	<i>Vireo olivaceus</i>	0.88	< 0.001	< 0.001	1.38	< 0.001	0.05
Carolina Chickadee	<i>Poecile carolinensis</i>	0.44	< 0.001	< 0.001	0.74	< 0.001	0.07
Tufted Titmouse	<i>Baeolophus bicolor</i>	0.60	< 0.001	< 0.001	0.99	< 0.001	0.08
White-breasted Nuthatch	<i>Sitta carolinensis</i>	0.48	< 0.001	< 0.001	0.71	< 0.001	0.20
Blue-gray Gnatcatcher	<i>Polioptila caerulea</i>	0.79	< 0.001	< 0.001	1.19	< 0.001	< 0.001
Wood Thrush	<i>Hylocichla mustelina</i>	0.69	< 0.001	< 0.001	1.21	< 0.001	0.12
Ovenbird	<i>Seiurus aurocapilla</i>	0.41	< 0.001	< 0.001	0.54	< 0.001	< 0.001
Kentucky Warbler	<i>Geothlypis Formosa</i>	0.41	< 0.001	< 0.001	0.50	< 0.001	0.001
Hooded Warbler	<i>Setophaga citrina</i>	0.28	< 0.001	< 0.001	0.32	< 0.001	0.29
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	0.38	< 0.001	< 0.001	0.56	< 0.001	0.25
Scarlet Tanager	<i>Piranga olivacea</i>	0.47	< 0.001	< 0.001	0.49	< 0.001	0.04
Northern Cardinal	<i>Cardinalis cardinalis</i>	0.42	< 0.001	< 0.001	0.64	< 0.001	0.01
Indigo Bunting	<i>Passerina cyanea</i>	0.22	< 0.001	< 0.001	0.25	< 0.001	0.21
Brown-headed Cowbird	<i>Molothrus ater</i>	0.69	< 0.001	< 0.001	0.98	< 0.001	0.01



**Figure 1.5** A comparison of the parameter estimates generated by open occupancy (left) and abundance (right) models fit to the confounded TE/dynamics and isolated TE empirical datasets for 19 forest-breeding songbirds. Error bars represent 95% Wald confidence intervals and the dashed line indicates no difference in estimates. P-values are the result of a pairwise t-test. Most parameter estimates were statistically indistinguishable under this sampling scheme when primary periods were separated by 2 days versus 17 days.



**Figure 1.6** A comparison of the parameter estimates generated by open occupancy (left) and abundance (right) models fit to the confounded TE/dynamics and isolated dynamics datasets for nine (occupancy) and eight (abundance) forest-breeding songbirds. Error bars represent 95% Wald confidence intervals and the dashed line indicates no difference in estimates. P-values are the result of a pairwise t-test. Most parameter estimates were statistically different when TE was adequately incorporated into the detection estimate.



**Figure 1.7** In order to quantify true population dynamics independently from temporary emigration (TE) rates, secondary samples should be spaced far enough apart in time such that probability of individual availability is independent on each repeated visit, but true changes in superpopulations are negligible. In (a), the gray box represents the maximum length of a primary sampling period, and three secondary samples are spaced so that probability of availability is independent on each occasion. If samples are conducted closer together in time, population dynamics will be confounded with TE rates. If secondary samples occur outside of the gray box, dynamic rates will be confounded with detection probability. In (b), TE and population dynamics occur at similar rates, and the two processes cannot be distinguished using Pollock's (1982) robust sampling design.

### Effects of Fragmentation on Avian Distributions, Dynamics, and Richness

Dynamic occupancy models were unfortunately not able to achieve convergence for 7 species (Yellow-throated Vireo, Summer Tanager, Blue Jay, Hairy Woodpecker, Carolina Chickadee, Carolina Wren, and Downy Woodpecker). Indeed, this became a problem with less common species as well, and thus the reason we truncated our analyses with these 30 common species. Initial occupancy was significantly influenced by one or more of the local vegetation principal components for 16 of the remaining 23 species, with PC 1 having influence on the most species (Table 1.10). Initial occupancy rates for 2 species were positively influenced by edge distance (Great-crested Flycatcher and Northern Flicker), and rates for 3 species negatively so (Common Yellowthroat, Indigo Bunting, and Yellow-breasted Chat). These latter 3 species are widely known to prefer forest edges (Rodewald 2015).

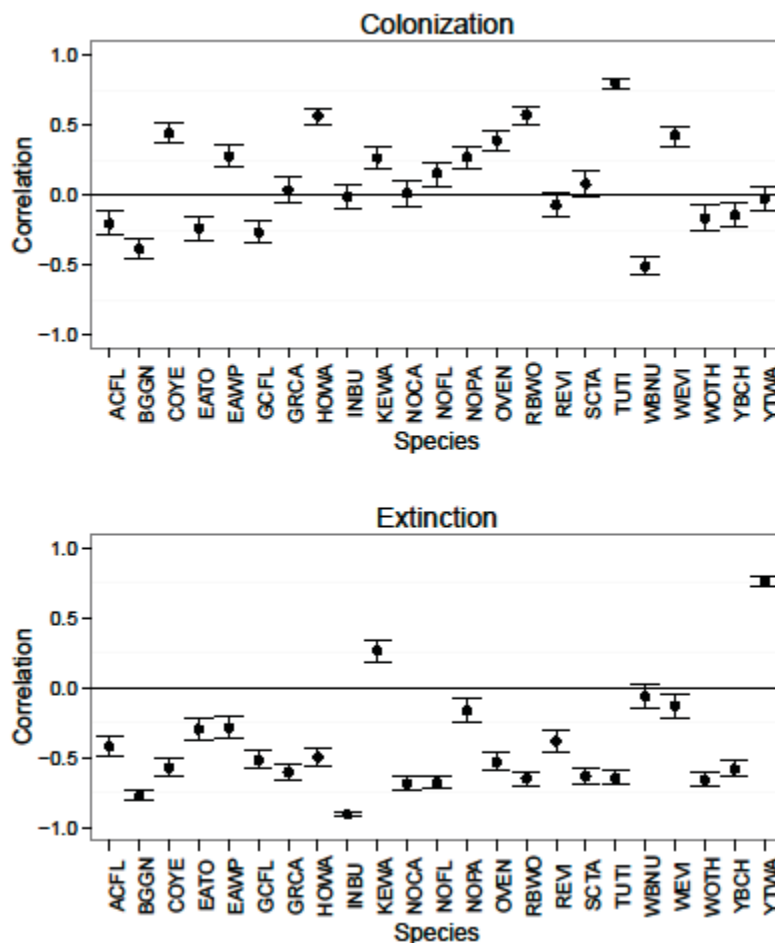
Initial occupancy of 16 species was significantly influenced by one or more of our landscape variables (habitat amount, patch size, or their interaction). The effect of patch size

increased as habitat amount decreased for only 7 species, but none of these effects was statistically significant, providing no support for the threshold hypothesis (Andren 1994; Fahrig 2003). The effect of patch size on initial occupancy was positive for only 8 species, and significantly positive for only 3. Occupancy rates for 2 additional species decreased significantly as patch size increased. Nonetheless, occupancy rates for 8 species were influenced by patch size in ways that could not be explained by habitat amount alone, suggesting that the habitat amount hypothesis (Fahrig 2013) may not be applicable for some species. Additionally, amount of habitat had a positive effect on initial occupancy for only 10 species, half of which were statistically significant. Occupancy rates for 8 species, on the other hand, were significantly negatively impacted by habitat amount.

Metapopulation theory predicts that colonization rates should increase as habitat amount increases, and that was true for the majority (12) of our 23 species. However, the effect of amount on colonization was only statistically significant for 3 species (Table 1.11). Similarly, extinction rates should decrease as patch size increases, and again that was true for the majority (14) of our species. However, this effect was only statistically significant for 4 species (Table 1.12). Patch

size effected colonization rates (beyond what could be explained by habitat amount) for 6 species, and on extinction rates for 7, again suggesting that the habitat amount hypothesis may not apply to some species.

If species distribution patterns are driven by inter-annual colonization and extinction rates, then we would expect to see strong positive correlation between predicted initial occupancy and colonization rates. This was true for 10 species, though we also saw significant negative correlation for 7 species (Figure 1.8). Similarly, we'd expect to see significant negative correlation between predicted initial occupancy and extinction rates, and this was, in fact true for the majority (20) of species (Figure 1.8).



**Figure 1.8** Pearson's correlation coefficients (and confidence intervals) for the relationship between predicted initial occupancy and predicted colonization (top) and extinction (bottom) rates for 23 species based on point counts conducted between 2011 and 2013.

**Table 1.10** Parameter estimates, standard errors, and tests of statistical significance for effects of covariates on initial occupancy for 23 species sampled during the breeding seasons of 2011-2013. Numbers highlighted in bold indicate statistically significant effects ( $\alpha = 0.05$ ).

Species	Int		PC1		PC2		PC3		Edge		Amount		Size		Size*Amount	
	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p
Aeolian Flycatcher	<b>1.91 (0.19)</b>	< <b>0.01</b>	<b>-0.44 (0.11)</b>	< <b>0.01</b>	<b>-0.38 (0.13)</b>	< <b>0.01</b>	0.03 (0.18)	0.85	0.34 (0.28)	0.23	0.13 (0.17)	0.45	0.07 (0.2)	0.74	<b>0.6 (0.19)</b>	< <b>0.01</b>
Blue-gray Gnatcatcher	<b>2.81 (0.46)</b>	< <b>0.01</b>	0.21 (0.21)	0.33	-0.21 (0.25)	0.4	0.34 (0.34)	0.32	-0.06 (0.23)	0.79	<b>-0.79 (0.37)</b>	<b>0.03</b>	-0.23 (0.4)	0.57	0 (0.32)	0.99
Common Yellowthroat	<b>-1.23 (0.19)</b>	< <b>0.01</b>	<b>0.3 (0.1)</b>	< <b>0.01</b>	<b>0.37 (0.13)</b>	<b>0.01</b>	0.12 (0.16)	0.45	<b>-0.88 (0.3)</b>	< <b>0.01</b>	0.12 (0.16)	0.46	<b>-0.5 (0.2)</b>	<b>0.01</b>	<b>0.46 (0.18)</b>	<b>0.01</b>
Eastern Towhee	<b>1.4 (0.21)</b>	< <b>0.01</b>	<b>0.7 (0.15)</b>	< <b>0.01</b>	0.01 (0.14)	0.95	<b>0.39 (0.17)</b>	<b>0.03</b>	-0.24 (0.16)	0.14	0.16 (0.17)	0.35	-0.32 (0.19)	0.1	-0.01 (0.16)	0.94
Eastern-wood Pewee	<b>0.99 (0.25)</b>	< <b>0.01</b>	-0.05 (0.12)	0.64	<b>-0.37 (0.16)</b>	<b>0.03</b>	-0.2 (0.21)	0.34	0.05 (0.19)	0.78	<b>-0.49 (0.2)</b>	<b>0.01</b>	-0.25 (0.24)	0.28	0.15 (0.19)	0.42
Great-crested Flycatcher	-0.34 (0.37)	0.36	<b>-0.47 (0.2)</b>	<b>0.02</b>	0.24 (0.21)	0.25	0.24 (0.25)	0.35	<b>0.75 (0.36)</b>	<b>0.04</b>	<b>-0.99 (0.26)</b>	< <b>0.01</b>	-0.36 (0.34)	0.29	-0.26 (0.31)	0.39
Gray Catbird	<b>-1.01 (0.18)</b>	< <b>0.01</b>	<b>0.21 (0.1)</b>	<b>0.04</b>	<b>0.35 (0.13)</b>	<b>0.01</b>	0.15 (0.16)	0.34	-0.06 (0.18)	0.75	<b>0.36 (0.15)</b>	<b>0.02</b>	-0.36 (0.2)	0.07	<b>0.42 (0.16)</b>	<b>0.01</b>
Hooded Warbler	<b>-1.41 (0.21)</b>	< <b>0.01</b>	<b>0.41 (0.12)</b>	< <b>0.01</b>	<b>-0.34 (0.15)</b>	<b>0.03</b>	-0.26 (0.19)	0.16	0.4 (0.27)	0.14	<b>1.2 (0.2)</b>	< <b>0.01</b>	<b>0.66 (0.24)</b>	<b>0.01</b>	-0.41 (0.21)	0.05
Indigo Bunting	<b>2.24 (0.31)</b>	< <b>0.01</b>	<b>0.49 (0.19)</b>	<b>0.01</b>	0.18 (0.2)	0.37	0.31 (0.25)	0.21	<b>-1.02 (0.24)</b>	< <b>0.01</b>	-0.28 (0.22)	0.21	0.24 (0.28)	0.4	-0.25 (0.2)	0.21
Kentucky Warbler	<b>1.09 (0.23)</b>	< <b>0.01</b>	<b>0.6 (0.16)</b>	< <b>0.01</b>	-0.25 (0.15)	0.1	0.02 (0.17)	0.92	0.28 (0.25)	0.27	0.07 (0.18)	0.69	-0.1 (0.24)	0.66	0.4 (0.22)	0.07
Northern Cardinal	<b>1.91 (0.22)</b>	< <b>0.01</b>	<b>0.42 (0.14)</b>	< <b>0.01</b>	-0.1 (0.16)	0.53	0.19 (0.18)	0.29	-0.21 (0.17)	0.21	<b>-0.86 (0.2)</b>	< <b>0.01</b>	-0.31 (0.22)	0.15	<b>0.44 (0.18)</b>	<b>0.01</b>
Northern Flicker	0.11 (0.51)	0.84	-0.17 (0.24)	0.48	-0.38 (0.29)	0.2	0.35 (0.4)	0.37	<b>0.86 (0.42)</b>	<b>0.04</b>	<b>-1.25 (0.5)</b>	<b>0.01</b>	-0.81 (0.61)	0.18	0.75 (0.58)	0.19
Northern Parula	<b>0.49 (0.21)</b>	<b>0.02</b>	0.01 (0.1)	0.88	0.02 (0.14)	0.89	0.11 (0.15)	0.47	-0.1 (0.17)	0.57	-0.05 (0.16)	0.77	-0.09 (0.19)	0.64	-0.01 (0.16)	0.95
Ovenbird	<b>-1.16 (0.21)</b>	< <b>0.01</b>	-0.21 (0.13)	0.09	-0.11 (0.16)	0.49	-0.22 (0.18)	0.22	0.43 (0.25)	0.08	<b>1.19 (0.22)</b>	< <b>0.01</b>	<b>0.96 (0.26)</b>	< <b>0.01</b>	0.07 (0.27)	0.79
Red-bellied Woodpecker	<b>0.56 (0.25)</b>	<b>0.02</b>	<b>-0.33 (0.14)</b>	<b>0.02</b>	<b>-0.46 (0.17)</b>	<b>0.01</b>	0.23 (0.22)	0.29	-0.06 (0.23)	0.81	<b>-1.06 (0.22)</b>	< <b>0.01</b>	0.02 (0.26)	0.92	0.35 (0.22)	0.11
Red-eyed Vireo	<b>3.05 (0.56)</b>	< <b>0.01</b>	<b>-0.35 (0.17)</b>	<b>0.04</b>	0.2 (0.28)	0.48	-0.06 (0.29)	0.83	0.17 (0.43)	0.69	<b>1.11 (0.4)</b>	<b>0.01</b>	-0.09 (0.41)	0.83	0.23 (0.34)	0.49
Scarlet Tanager	<b>0.96 (0.25)</b>	< <b>0.01</b>	0.13 (0.15)	0.39	-0.25 (0.17)	0.14	-0.35 (0.2)	0.08	0.28 (0.28)	0.31	<b>0.5 (0.19)</b>	<b>0.01</b>	<b>0.67 (0.28)</b>	<b>0.02</b>	-0.06 (0.22)	0.8
Tufted Titmouse	<b>2.38 (0.58)</b>	< <b>0.01</b>	-0.25 (0.17)	0.13	-0.13 (0.22)	0.54	0.26 (0.3)	0.39	-0.32 (0.22)	0.15	<b>-1.38 (0.43)</b>	< <b>0.01</b>	-0.02 (0.68)	0.98	0.14 (0.51)	0.79
White-breasted Nuthatch	<b>1.25 (0.34)</b>	< <b>0.01</b>	<b>-0.28 (0.15)</b>	<b>0.05</b>	<b>-0.45 (0.21)</b>	<b>0.03</b>	-0.45 (0.26)	0.08	0.08 (0.28)	0.78	<b>-1.12 (0.26)</b>	< <b>0.01</b>	-0.38 (0.37)	0.31	0.25 (0.26)	0.32
White-eyed Vireo	<b>-0.9 (0.16)</b>	< <b>0.01</b>	<b>0.41 (0.1)</b>	< <b>0.01</b>	<b>0.33 (0.12)</b>	<b>0.01</b>	0.28 (0.15)	0.05	-0.32 (0.21)	0.13	<b>0.47 (0.15)</b>	< <b>0.01</b>	<b>-0.62 (0.19)</b>	< <b>0.01</b>	0.21 (0.15)	0.17
Wood Thrush	<b>0.51 (0.17)</b>	< <b>0.01</b>	0.19 (0.11)	0.07	<b>-0.36 (0.12)</b>	< <b>0.01</b>	0.15 (0.14)	0.28	0.43 (0.23)	0.06	-0.16 (0.13)	0.22	0.31 (0.18)	0.07	0 (0.14)	0.99
Yellow-breasted Chat	<b>-0.49 (0.22)</b>	<b>0.03</b>	<b>0.44 (0.13)</b>	< <b>0.01</b>	0.24 (0.16)	0.13	0.15 (0.19)	0.43	<b>-0.57 (0.27)</b>	<b>0.04</b>	-0.23 (0.19)	0.21	-0.28 (0.25)	0.27	0.34 (0.21)	0.1
Yellow-throated Warbler	-0.08 (0.3)	0.79	-0.13 (0.13)	0.29	0.12 (0.16)	0.45	-0.06 (0.18)	0.75	0.06 (0.21)	0.76	-0.26 (0.2)	0.2	-0.23 (0.23)	0.33	-0.35 (0.21)	0.1



**Table 1.11** Parameter estimates, standard errors, and tests of statistical significance for effects of covariates on inter-annual colonization rates for 23 species sampled during the breeding seasons of 2011–2013. Numbers highlighted in bold indicate statistically significant effects ( $\alpha = 0.05$ ).

Species	Int		Edge		Amount		Size		Size*Amount	
	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p
Acadian Flycatcher	<b>-0.62 (0.25)</b>	<b>0.01</b>	-0.16 (0.38)	0.67	-0.25 (0.24)	0.3	0.13 (0.26)	0.61	-0.08 (0.27)	0.77
Blue-gray Gnatcatcher	-1.09 (0.97)	0.26	-1.15 (0.69)	0.09	0.51 (0.78)	0.51	0.55 (0.79)	0.49	0.02 (0.67)	0.97
Common Yellowthroat	<b>-2.49 (0.27)</b>	<b>&lt; 0.01</b>	<b>-1.07 (0.33)</b>	<b>&lt; 0.01</b>	-0.32 (0.25)	0.19	0.42 (0.25)	0.09	0.36 (0.23)	0.12
Eastern Towhee	<b>-1.12 (0.31)</b>	<b>&lt; 0.01</b>	-0.15 (0.21)	0.47	-0.25 (0.24)	0.29	0.25 (0.29)	0.39	0.28 (0.2)	0.16
Eastern-wood Pewee	-0.3 (0.3)	0.32	-0.08 (0.28)	0.78	0.09 (0.32)	0.77	-0.33 (0.39)	0.4	0.47 (0.32)	0.15
Great-crested Flycatcher	<b>-1.04 (0.39)</b>	<b>0.01</b>	-0.18 (0.4)	0.66	0.26 (0.32)	0.41	-0.62 (0.39)	0.11	0.14 (0.3)	0.64
Gray Catbird	<b>-6 (1.43)</b>	<b>&lt; 0.01</b>	<b>-6.4 (2.15)</b>	<b>&lt; 0.01</b>	-0.1 (0.3)	0.73	0.37 (0.32)	0.26	<b>-0.76 (0.36)</b>	<b>0.03</b>
Hooded Warbler	<b>-4.29 (0.97)</b>	<b>&lt; 0.01</b>	0.64 (0.45)	0.16	<b>1.34 (0.59)</b>	<b>0.02</b>	<b>1.15 (0.56)</b>	<b>0.04</b>	<b>-1.4 (0.55)</b>	<b>0.01</b>
Indigo Bunting	<b>-2.71 (0.84)</b>	<b>&lt; 0.01</b>	0.87 (0.48)	0.07	<b>1.38 (0.5)</b>	<b>0.01</b>	<b>-3.62 (1.3)</b>	<b>0.01</b>	<b>2.22 (0.75)</b>	<b>&lt; 0.01</b>
Kentucky Warbler	<b>-1.49 (0.39)</b>	<b>&lt; 0.01</b>	0.55 (0.41)	0.18	0.34 (0.27)	0.21	0.24 (0.43)	0.57	0.01 (0.28)	0.97
Northern Cardinal	-0.01 (0.3)	0.96	-0.07 (0.19)	0.71	-0.08 (0.24)	0.74	0.15 (0.47)	0.75	-0.32 (0.34)	0.36
Northern Flicker	-0.08 (0.61)	0.9	-1.33 (1.33)	0.32	-0.94 (0.48)	0.05	-0.34 (0.65)	0.6	-0.99 (0.8)	0.21
Northern Parula	<b>-1.64 (0.43)</b>	<b>&lt; 0.01</b>	0.13 (0.37)	0.74	-0.34 (0.35)	0.32	0.01 (0.37)	0.98	-0.21 (0.3)	0.48
Ovenbird	<b>-4.44 (1.39)</b>	<b>&lt; 0.01</b>	-1.9 (1.99)	0.34	<b>1.13 (0.45)</b>	<b>0.01</b>	0.18 (0.46)	0.7	<b>1 (0.45)</b>	<b>0.03</b>
Red-bellied Woodpecker	0.21 (0.37)	0.58	0.36 (0.28)	0.19	-0.41 (0.31)	0.19	0.19 (0.41)	0.65	-0.06 (0.36)	0.87
Red-eyed Vireo	1.39 (0.99)	0.16	2.74 (2.17)	0.21	-0.41 (0.46)	0.38	-0.66 (0.76)	0.39	-0.05 (0.46)	0.91
Scarlet Tanager	-1.19 (0.71)	0.09	<b>-4.3 (1.69)</b>	<b>0.01</b>	0.32 (0.53)	0.55	<b>2.09 (0.86)</b>	<b>0.01</b>	-0.5 (0.49)	0.3
Tufted Titmouse	4.3 (2.39)	0.07	-0.29 (0.39)	0.46	-2.39 (1.51)	0.11	-1.3 (1.13)	0.25	1.27 (0.75)	0.09
White-breasted Nuthatch	0.15 (0.39)	0.71	0.36 (0.34)	0.29	0.22 (0.36)	0.53	-0.03 (0.31)	0.94	-0.13 (0.25)	0.6
White-eyed Vireo	<b>-2.34 (0.22)</b>	<b>&lt; 0.01</b>	-0.18 (0.21)	0.4	0.06 (0.18)	0.73	-0.3 (0.25)	0.23	<b>0.44 (0.18)</b>	<b>0.01</b>
Wood Thrush	<b>-1.19 (0.25)</b>	<b>&lt; 0.01</b>	-0.44 (0.47)	0.36	0.43 (0.23)	0.06	0.32 (0.23)	0.17	-0.06 (0.22)	0.79
Yellow-breasted Chat	<b>-2.83 (0.44)</b>	<b>&lt; 0.01</b>	-0.21 (0.29)	0.47	-0.09 (0.37)	0.81	0.36 (0.53)	0.49	0.03 (0.45)	0.95
Yellow-throated Warbler	<b>-3.09 (0.95)</b>	<b>&lt; 0.01</b>	-0.78 (1.22)	0.52	0.18 (0.57)	0.76	-0.14 (0.63)	0.82	0.29 (0.41)	0.48

**Table 1.12** Parameter estimates, standard errors, and tests of statistical significance for effects of covariates on inter-annual extinction rates for 23 species sampled during the breeding seasons of 2011–2013. Numbers highlighted in bold indicate statistically significant effects ( $\alpha = 0.05$ ).

Species	Int		Edge		Amount		Size		Size*Amount	
	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p	Est (SE)	p
Acadian Flycatcher	<b>-3.62 (0.42)</b>	< <b>0.01</b>	-0.4 (0.5)	0.43	0.51 (0.31)	0.11	-0.56 (0.41)	0.18	0 (0.33)	0.99
Blue-gray Gnatcatcher	<b>-3.45 (1.4)</b>	<b>0.01</b>	-0.25 (0.2)	0.22	1.08 (1.25)	0.39	1.19 (0.67)	0.07	-0.36 (0.65)	0.58
Common Yellowthroat	-0.51 (0.34)	0.13	0.76 (0.54)	0.16	-0.15 (0.28)	0.58	-0.01 (0.31)	0.98	0.21 (0.29)	0.47
Eastern Towhee	<b>-2.32 (0.26)</b>	< <b>0.01</b>	0.05 (0.22)	0.81	<b>0.6 (0.25)</b>	<b>0.01</b>	0.26 (0.27)	0.34	0.03 (0.22)	0.89
Eastern-wood Pewee	<b>-2.49 (0.48)</b>	< <b>0.01</b>	-0.66 (0.6)	0.27	0.53 (0.34)	0.11	-0.34 (0.48)	0.48	0.04 (0.4)	0.92
Great-crested Flycatcher	-1.05 (1.04)	0.31	0.03 (0.42)	0.94	<b>1.95 (0.95)</b>	<b>0.04</b>	-2.15 (1.28)	0.09	1.75 (1.2)	0.14
Gray Catbird	-0.23 (0.3)	0.45	0.16 (0.24)	0.49	-0.56 (0.3)	0.06	<b>0.83 (0.33)</b>	<b>0.01</b>	-0.26 (0.26)	0.32
Hooded Warbler	-0.92 (0.53)	0.08	0.16 (0.45)	0.72	-0.91 (0.79)	0.25	-0.29 (0.64)	0.65	-1.21 (1.04)	0.24
Indigo Bunting	<b>-1.71 (0.18)</b>	< <b>0.01</b>	<b>0.82 (0.2)</b>	< <b>0.01</b>	0.14 (0.17)	0.42	-0.32 (0.22)	0.14	0.29 (0.15)	0.05
Kentucky Warbler	<b>-4.8 (1.47)</b>	< <b>0.01</b>	0.41 (0.37)	0.27	1.98 (1.04)	0.06	<b>-2.72 (1.12)</b>	<b>0.02</b>	<b>2.18 (0.72)</b>	< <b>0.01</b>
Northern Cardinal	<b>-3.33 (0.7)</b>	< <b>0.01</b>	<b>0.54 (0.26)</b>	<b>0.04</b>	<b>2.14 (0.52)</b>	< <b>0.01</b>	-0.85 (0.73)	0.24	0.5 (0.46)	0.28
Northern Flicker	-0.18 (0.63)	0.78	<b>-2.17 (0.99)</b>	<b>0.03</b>	0.56 (0.52)	0.28	0.74 (0.67)	0.27	-0.29 (0.38)	0.44
Northern Parula	<b>-1.34 (0.31)</b>	< <b>0.01</b>	-0.23 (0.37)	0.53	-0.06 (0.26)	0.82	0.42 (0.28)	0.14	-0.21 (0.29)	0.47
Ovenbird	<b>-2.68 (1.03)</b>	<b>0.01</b>	<b>-5.08 (1.7)</b>	< <b>0.01</b>	-1.01 (0.75)	0.18	<b>-1.72 (0.77)</b>	<b>0.03</b>	<b>3.26 (1.05)</b>	< <b>0.01</b>
Red-bellied Woodpecker	<b>-1.54 (0.32)</b>	< <b>0.01</b>	0.2 (0.21)	0.34	<b>1.12 (0.26)</b>	< <b>0.01</b>	<b>0.78 (0.35)</b>	<b>0.03</b>	<b>-1.25 (0.35)</b>	< <b>0.01</b>
Red-eyed Vireo	<b>-3.37 (0.51)</b>	< <b>0.01</b>	-1.02 (0.89)	0.25	-0.55 (0.29)	0.06	<b>-0.71 (0.32)</b>	<b>0.03</b>	-0.27 (0.3)	0.37
Scarlet Tanager	<b>-2.14 (1.04)</b>	<b>0.04</b>	-3.29 (1.72)	0.06	<b>-0.99 (0.39)</b>	<b>0.01</b>	0.3 (0.35)	0.39	-0.59 (0.36)	0.1
Tufted Titmouse	<b>-2.66 (0.5)</b>	< <b>0.01</b>	-0.29 (0.23)	0.2	<b>1.25 (0.39)</b>	< <b>0.01</b>	-0.56 (0.38)	0.14	<b>1.07 (0.32)</b>	< <b>0.01</b>
White-breasted Nuthatch	<b>-3.99 (1.66)</b>	<b>0.02</b>	0.89 (0.83)	0.29	1.4 (1.2)	0.25	<b>-2.81 (1.15)</b>	<b>0.01</b>	1.19 (1)	0.23
White-eyed Vireo	<b>-1.19 (0.26)</b>	< <b>0.01</b>	0.56 (0.36)	0.12	-0.04 (0.26)	0.88	-0.47 (0.34)	0.16	0.34 (0.25)	0.17
Wood Thrush	<b>-1.52 (0.24)</b>	< <b>0.01</b>	-0.56 (0.3)	0.07	0.35 (0.19)	0.07	-0.11 (0.29)	0.71	-0.07 (0.25)	0.79
Yellow-breasted Chat	-0.06 (0.28)	0.82	0.76 (0.44)	0.09	-0.25 (0.2)	0.22	0.18 (0.29)	0.52	-0.07 (0.23)	0.77
Yellow-throated Warbler	-0.43 (0.37)	0.24	-0.21 (0.3)	0.47	-0.17 (0.27)	0.54	0.07 (0.31)	0.82	-0.38 (0.38)	0.31

For our community analysis, we determined that 72 recorded species actually breed in the region and can be reasonably sampled with point counts. Of those 72 species, we classified 21 as forest edge specialists, 23 as forest generalists, and 8 as forest interior specialists; the other 20 species were considered habitat generalists and excluded from modeling (Table 1.2). We found very little evidence that the effect of forest patch size changed as a function of the amount of forest in the local landscape. Credible intervals for the patch.size-by-amount interaction term overlapped zero for the community mean of all three habitat groups, and for 46 (88%) of 52 species. We found no evidence for lack of fit in the model that included the interaction term ( $p = 0.571$ ), nor in the model that excluded this term ( $p = 0.568$ ). In fact, the posterior distributions for all parameters shared between the two models were nearly identical. Therefore, we present the results from the simpler model below, as interpretation of those parameter estimates is more straightforward.

Estimates for the effects of patch size per se on occupancy rates revealed substantial differences in the response of habitat groups to fragmentation. The estimate of the average patch size effect was significantly positive for interior specialists, significantly negative for edge specialists, and approximately zero for habitat generalists (Fig. 1.9). In fact, 78% of species that were significantly positively associated with patch size were interior specialists, and 86% that were significantly negatively associated with patch size were edge specialists. These results were also reflected in emergent patterns of species richness. Predicted richness values increased with patch size for interior specialists, and decreased with patch size for edge specialists, while there was no strong trend for forest generalists or for all species combined (Fig. 1.10).

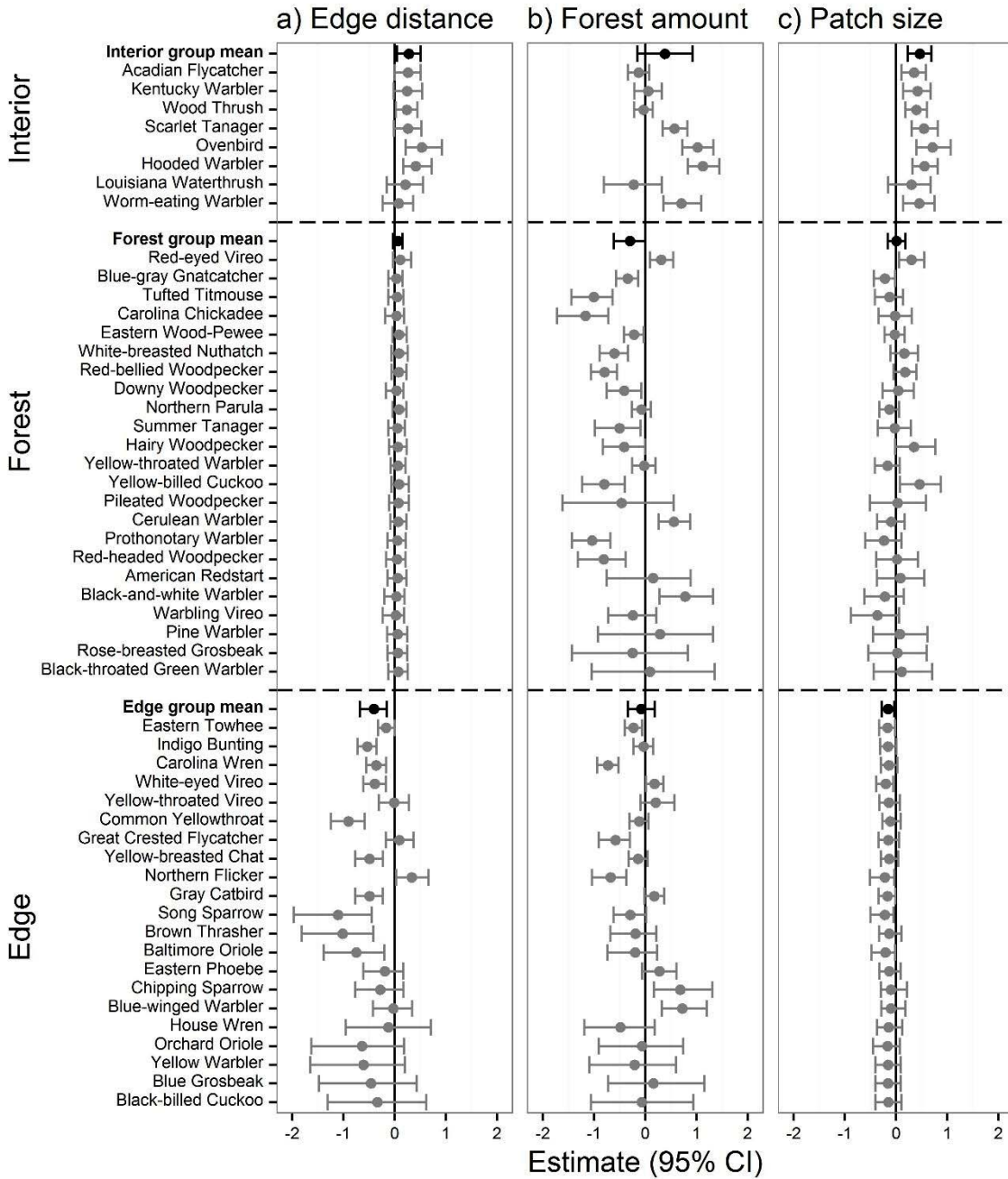
The effects of forest amount were much more variable within habitat groups; the credible intervals for the average effect of forest amount overlapped zero for all groups (Fig. 1.9). Nonetheless, a much greater proportion of interior species were significantly positively associated with forest amount (50%), when compared to the generalist (13%) and edge (14%) groups. Surprisingly, 16 total species were significantly negatively associated with the amount of forest within 2 km, including over half of the forest generalists. Of these 16 species, 11 (69%) are obligate primary (Downy Woodpecker, Hairy Woodpecker, Red-bellied Woodpecker, Red-headed Woodpecker, and Northern Flicker) or secondary (Carolina Chickadee, Prothonotary Warbler, Tufted Titmouse, White-breasted Nuthatch, Carolina Wren, and Great Crested Flycatcher) cavity nesters (Rodewald 2015). Again, these results were reflected in the emergent richness patterns; while predicted richness of interior species increased with increasing forest cover, predicted richness of edge specialists, forest generalists, and all species combined was actually greatest at low forest cover values (Fig. 1.10).

At a finer scale, one or more local habitat covariates (edge distance, PC1, PC2, or PC3) influenced the probability of occupancy for 26 (50%) species (Table 1.13). In fact, the estimates of the effects of edge distance confirmed that our habitat group classifications were relatively accurate. On average, probability of occupancy was greater at points further from the edge for interior specialists, and greater at points close to the edge for edge specialists; for all 23 forest generalists, the credible intervals for the effect of edge distance overlapped zero (Fig. 1.10).

**Table 1.13.** Means and 95% credible intervals for the posterior distributions of covariate effects on occupancy probabilities of 52 breeding bird species. Species were separated into habitat groups (edge specialists, forest generalists, or interior specialists), and rows highlighted in bold represent the estimated mean effect of the covariate on members of the habitat group. Within a habitat group, species are listed from most common (top) to least common (Table 1.2). The 95% credible intervals did not overlap zero for those entries marked with an asterisk.

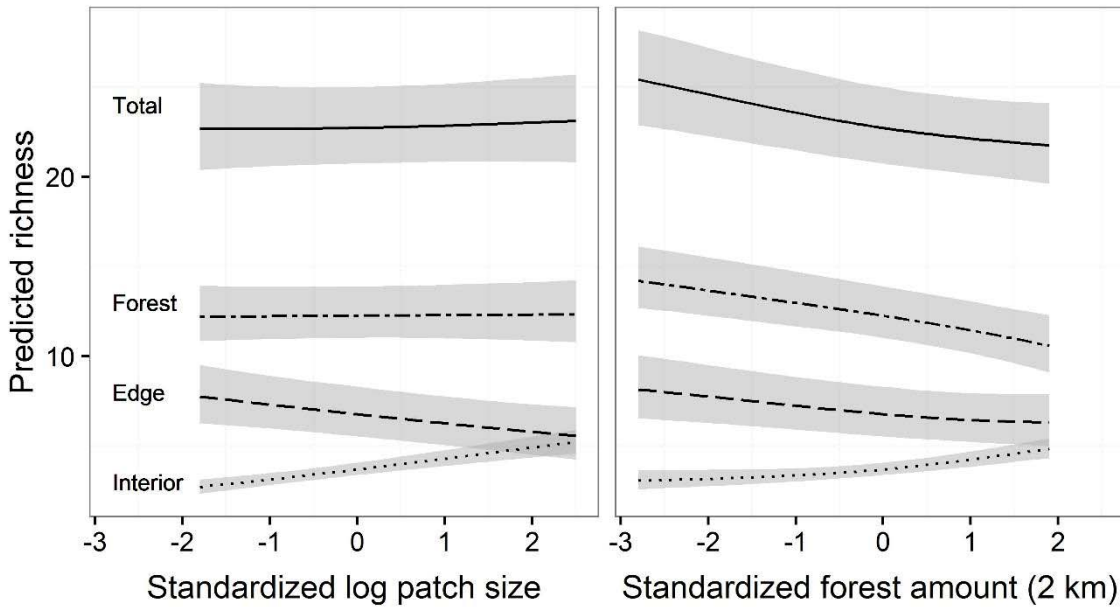
Species	Intercept (year = 1)	Intercept (year ≥ 1)	Autologistic	PCI	PC2	PC3	Edge distance	Patch size	Forest amount
<b>Edge community</b>									
Eastern Towhee	-1.05 (-1.98, -0.22)*	-1.95 (-2.77, -1.15)*	2.78 (2.16, 3.64)*	0.20 (0.09, 0.30)*	0.10 (0.02, 0.20)*	0.05 (-0.05, 0.13)	-0.40 (-0.68, -0.15)*	-0.16 (-0.28, -0.04)*	-0.08 (-0.33, 0.18)
Indigo Bunting	1.17 (0.88, 1.49)*	-0.41 (-0.79, -0.04)*	2.51 (1.91, 3.10)*	0.42 (0.29, 0.57)*	0.02 (-0.14, 0.15)	0.05 (-0.06, 0.17)	-0.17 (-0.33, -0.00)*	-0.17 (-0.33, -0.02)*	-0.23 (-0.41, -0.06)*
Carolina Wren	1.85 (1.46, 2.28)*	-0.75 (-1.30, -0.25)*	2.63 (1.96, 3.35)*	0.33 (0.18, 0.48)*	0.11 (-0.03, 0.26)	0.04 (-0.08, 0.16)	-0.53 (-0.72, -0.35)*	-0.16 (-0.31, 0.01)	-0.04 (-0.23, 0.16)
White-eyed Vireo	0.05 (-0.27, 0.39)	0.30 (-0.06, 0.69)	2.22 (1.33, 3.02)*	0.26 (0.13, 0.41)*	0.12 (-0.02, 0.27)	0.08 (-0.03, 0.25)	-0.36 (-0.55, -0.16)*	-0.14 (-0.29, 0.03)	-0.73 (-0.94, -0.53)*
Yellow-throated Vireo	-0.95 (-1.23, -0.67)*	-2.13 (-2.48, -1.80)*	3.05 (2.46, 3.76)*	0.25 (0.14, 0.37)*	0.04 (-0.10, 0.16)	0.08 (-0.04, 0.22)	-0.39 (-0.61, -0.17)*	-0.20 (-0.39, -0.05)*	0.18 (0.01, 0.35)*
Common Yellowthroat	0.26 (-0.31, 0.93)	-0.33 (-1.09, 0.72)	3.06 (1.80, 5.33)*	-0.04 (-0.26, 0.20)	0.06 (0.13, 0.24)	0.03 (-0.14, 0.16)	-0.01 (-0.31, 0.29)	-0.14 (-0.32, 0.07)	0.20 (-0.10, 0.57)
Great Crested Flycatcher	-1.03 (-1.39, -0.66)*	-2.50 (-2.92, -2.10)*	2.52 (1.87, 3.16)*	0.20 (0.08, 0.33)*	0.14 (0.02, 0.29)*	0.05 (-0.08, 0.17)	-0.91 (-1.24, -0.59)*	-0.11 (-0.27, 0.08)	-0.12 (-0.31, 0.06)
Yellow-breasted Chat	-0.31 (-0.98, 0.45)	-0.27 (-1.02, 0.77)	2.26 (0.46, 3.87)*	0.03 (-0.20, 0.25)	0.13 (-0.04, 0.33)	0.06 (-0.07, 0.21)	0.09 (-0.17, 0.37)	-0.15 (-0.34, 0.06)	-0.59 (-0.91, -0.30)*
Northern Flicker	-1.04 (-1.41, -0.68)*	-2.57 (-2.97, -2.17)*	2.46 (1.82, 3.08)*	0.33 (0.20, 0.47)*	0.15 (0.02, 0.30)*	0.04 (-0.09, 0.16)	-0.49 (-0.77, -0.22)*	-0.14 (-0.29, 0.04)	-0.14 (-0.33, 0.05)
Gray Catbird	-0.33 (-1.06, 0.49)	-0.16 (-0.85, 0.75)	2.21 (-0.11, 3.95)	0.10 (-0.12, 0.30)	0.01 (-0.25, 0.18)	0.04 (-0.13, 0.18)	0.34 (0.03, 0.66)*	-0.22 (-0.51, -0.04)*	-0.68 (-1.04, -0.37)*
Song Sparrow	-1.23 (-1.59, -0.86)*	-2.68 (-3.12, -2.29)*	2.71 (2.02, 3.48)*	0.18 (0.04, 0.31)*	0.13 (0.00, 0.27)*	0.05 (-0.09, 0.17)	-0.49 (-0.77, -0.23)*	-0.17 (-0.34, -0.01)*	0.17 (-0.02, 0.36)
Brown Thrasher	-3.17 (-3.96, -2.39)*	-3.66 (-4.52, -2.89)*	3.65 (2.35, 6.11)*	0.18 (-0.02, 0.37)	0.15 (-0.02, 0.37)	0.02 (-0.17, 0.15)	-1.10 (-1.97, -0.45)*	-0.22 (-0.50, -0.04)*	-0.30 (-0.62, 0.02)
Baltimore Oriole	-1.41 (-2.06, -0.77)*	-2.37 (-3.60, -1.04)*	2.99 (1.55, 5.24)*	0.25 (0.00, 0.53)*	0.19 (0.01, 0.48)*	0.03 (-0.16, 0.16)	-1.02 (-1.81, -0.41)*	-0.14 (-0.33, 0.10)	-0.19 (-0.68, 0.21)
Eastern Phoebe	-1.07 (-2.47, 0.60)	-2.48 (-3.68, -1.14)*	3.01 (1.58, 5.24)*	0.20 (-0.05, 0.46)	0.04 (-0.22, 0.23)	0.04 (-0.14, 0.17)	-0.75 (-1.39, -0.20)*	-0.21 (-0.49, -0.02)*	-0.20 (-0.74, 0.23)
Chipping Sparrow	-2.88 (-3.77, -1.78)*	-3.41 (-4.22, -2.49)*	3.44 (2.23, 5.65)*	0.17 (-0.04, 0.37)	0.05 (-0.17, 0.22)	0.04 (-0.11, 0.19)	-0.19 (-0.61, 0.17)	-0.14 (-0.32, 0.09)	0.28 (-0.06, 0.61)
Blue-winged Warbler	-2.20 (-1.92, 1.95)	-2.37 (-3.94, -0.63)*	2.73 (-0.43, 5.23)	0.19 (-0.09, 0.48)	0.15 (-0.04, 0.43)	0.03 (-0.16, 0.18)	-0.28 (-0.77, 0.18)	-0.10 (-0.29, 0.21)	0.68 (0.17, 1.31)*
House Wren	-2.23 (-3.28, -1.03)*	-3.41 (-4.36, -2.36)*	2.68 (1.15, 4.58)*	0.26 (0.05, 0.48)*	0.13 (-0.05, 0.34)	0.05 (-0.12, 0.19)	-0.03 (-0.42, 0.34)	-0.10 (-0.29, 0.18)	0.72 (0.32, 1.20)*
Orchard Oriole	-1.52 (-3.88, 1.18)	-1.41 (-3.65, 1.14)	3.07 (1.32, 5.72)*	0.11 (-0.26, 0.43)	0.14 (-0.08, 0.45)	0.04 (-0.15, 0.19)	-0.12 (-0.96, 0.72)	-0.14 (-0.37, 0.12)	-0.49 (-1.19, 0.18)
Yellow Warbler	-1.08 (-3.52, 1.78)	-1.85 (-4.07, 0.71)	2.89 (1.07, 5.36)*	0.16 (-0.19, 0.48)	0.11 (-0.13, 0.38)	0.06 (-0.10, 0.24)	-0.63 (-1.63, 0.18)	-0.17 (-0.44, 0.08)	-0.07 (-0.91, 0.75)
Blue Grosbeak	-2.19 (-5.94, 1.38)	-3.14 (-5.40, -0.40)*	2.66 (0.71, 4.60)*	0.22 (-0.10, 0.56)	0.09 (-0.16, 0.35)	0.05 (-0.13, 0.21)	-0.61 (-1.65, 0.20)	-0.16 (-0.40, 0.09)	-0.21 (-1.09, 0.60)
Black-billed Cuckoo	-2.22 (-5.74, 1.14)	-3.21 (-6.42, -0.19)*	2.84 (0.89, 5.13)*	0.18 (-0.17, 0.50)	0.11 (-0.14, 0.37)	0.05 (-0.13, 0.21)	-0.46 (-1.48, 0.44)	-0.16 (-0.40, 0.09)	0.15 (-0.73, 1.15)
			2.65 (0.47, 4.85)*	0.19 (-0.17, 0.54)	0.10 (-0.14, 0.37)	0.05 (-0.13, 0.20)	-0.33 (-1.30, 0.62)	-0.15 (-0.40, 0.11)	-0.07 (-1.06, 0.94)
<b>Forest community</b>									
Red-eyed Vireo	0.11 (-1.29, 1.44)	-1.33 (-2.68, 0.08)	2.93 (1.82, 4.26)*	0.04 (-0.05, 0.12)	-0.12 (-0.20, -0.03)*	-0.02 (-0.17, 0.13)	0.06 (-0.04, 0.16)	0.01 (-0.16, 0.19)	-0.30 (-0.61, 0.00)
Blue-gray Gnatcatcher	2.48 (2.12, 2.88)*	1.51 (0.99, 2.06)*	1.24 (0.63, 1.84)*	-0.17 (-0.32, -0.03)*	-0.12 (-0.24, 0.01)	-0.32 (-0.55, -0.11)*	0.11 (-0.03, 0.32)	0.30 (0.06, 0.55)*	0.31 (0.09, 0.54)*
Tufted Titmouse	2.02 (1.66, 2.42)*	0.47 (0.01, 0.93)*	1.73 (1.01, 2.49)*	0.13 (0.00, 0.26)*	-0.12 (-0.25, -0.00)*	0.15 (-0.05, 0.35)	0.04 (-0.12, 0.16)	-0.22 (-0.43, -0.02)*	-0.35 (-0.57, -0.14)*
Carolina Chickadee	3.33 (2.28, 4.90)*	1.79 (0.59, 3.14)*	1.10 (-0.62, 3.05)	0.05 (-0.12, 0.23)	-0.11 (-0.26, 0.04)	0.23 (-0.07, 0.53)	0.04 (-0.12, 0.17)	-0.13 (-0.41, 0.14)	-1.01 (-1.44, -0.64)*
Eastern Wood-Pewee	1.07 (0.70, 1.47)*	-0.49 (-0.96, -0.07)*	2.70 (1.96, 3.56)*	-0.03 (-0.15, 0.09)	-0.13 (-0.29, 0.02)	0.10 (-0.23, 0.44)	0.03 (-0.18, 0.18)	-0.02 (-0.35, 0.31)	-1.17 (-1.73, -0.72)*
White-breasted Nuthatch	1.04 (0.60, 1.53)*	1.04 (0.38, 1.78)*	1.87 (0.65, 3.51)*	-0.10 (-0.27, 0.07)	-0.15 (-0.29, -0.02)*	-0.25 (-0.48, -0.04)*	0.09 (-0.04, 0.24)	-0.03 (-0.23, 0.17)	-0.22 (-0.42, -0.03)*
Red-bellied Woodpecker	0.75 (0.28, 1.30)*	0.53 (-0.11, 1.20)	1.05 (0.13, 2.14)*	0.03 (-0.12, 0.17)	-0.16 (-0.32, -0.03)*	-0.17 (-0.44, 0.09)	0.08 (-0.06, 0.25)	0.16 (-0.10, 0.43)	-0.61 (-0.89, -0.33)*
Downy Woodpecker	1.84 (1.05, 2.96)*	0.28 (-1.67, 1.93)	2.20 (-0.12, 5.31)	0.10 (-0.08, 0.29)	-0.11 (-0.27, 0.04)	-0.11 (-0.43, 0.20)	0.03 (-0.17, 0.18)	0.04 (-0.26, 0.34)	-0.80 (-1.06, -0.55)*
Summer Parula	0.28 (-0.05, 0.62)	-1.80 (-2.37, -1.32)*	3.15 (2.35, 4.10)*	0.11 (-0.01, 0.23)	-0.03 (-0.16, 0.14)	-0.01 (-0.19, 0.17)	0.08 (-0.04, 0.23)	0.18 (-0.05, 0.40)	-0.41 (-0.76, -0.08)*
Northern Tanager	1.23 (0.54, 2.08)*	-2.52 (-5.15, -0.42)*	5.92 (2.49, 10.28)*	0.02 (-0.17, 0.21)	-0.14 (-0.32, -0.00)*	-0.29 (-0.66, 0.05)	0.05 (-0.12, 0.20)	-0.13 (-0.32, 0.06)	-0.07 (-0.26, 0.11)
Hairy Woodpecker	-1.96 (-2.66, -1.27)*	1.35 (0.44, 2.81)*	1.25 (-1.14, 5.88)	0.10 (-0.08, 0.32)	-0.15 (-0.34, -0.01)*	0.11 (-0.24, 0.49)	0.06 (-0.11, 0.24)	-0.03 (-0.35, 0.29)	-0.50 (-0.99, -0.09)*
Yellow-throated Warbler	-0.16 (-0.70, 0.44)	-2.78 (-4.28, -1.89)*	3.36 (1.83, 5.63)*	0.03 (-0.11, 0.17)	-0.08 (-0.21, 0.07)	-0.04 (-0.30, 0.21)	0.07 (-0.08, 0.21)	0.35 (-0.02, 0.77)	-0.41 (-0.83, -0.01)*
Yellow-billed Cuckoo	4.02 (1.90, 7.77)*	-4.56 (-7.15, -2.67)*	4.19 (2.22, 6.85)*	0.07 (-0.11, 0.26)	-0.09 (-0.24, 0.09)	0.17 (-0.15, 0.53)	0.09 (-0.06, 0.28)	-0.17 (-0.41, 0.07)	-0.02 (-0.25, 0.20)
Pileated Woodpecker	4.01 (1.59, 7.99)*	1.25 (-2.95, 6.47)	3.62 (-0.44, 8.38)	0.03 (-0.22, 0.28)	-0.12 (-0.32, 0.07)	-0.02 (-0.53, 0.50)	0.08 (-0.11, 0.28)	0.03 (-0.51, 0.59)	-0.47 (-1.62, 0.56)
Cerulean Warbler	-3.99 (-5.32, -3.11)*	-3.99 (-5.32, -3.11)*	5.24 (3.32, 8.23)*	0.04 (-0.13, 0.20)	-0.13 (-0.29, 0.01)	-0.24 (-0.53, 0.04)	0.07 (-0.08, 0.23)	-0.09 (-0.37, 0.17)	0.56 (0.26, 0.87)*
Prothonotary Warbler	-2.88 (-3.53, -2.25)*	-4.53 (-5.69, -3.70)*	4.11 (2.45, 6.50)*	0.01 (-0.16, 0.19)	-0.10 (-0.25, 0.06)	0.14 (-0.15, 0.45)	0.05 (-0.14, 0.22)	-0.23 (-0.60, 0.10)	-1.04 (-1.43, -0.68)*
Red-headed Woodpecker	-1.36 (-2.79, 0.62)	-3.46 (-5.15, -1.90)*	2.45 (0.17, 5.11)*	0.05 (-0.15, 0.27)	-0.10 (-0.26, 0.09)	-0.05 (-0.42, 0.30)	0.05 (-0.16, 0.21)	0.02 (-0.39, 0.42)	-0.82 (-1.32, -0.38)*
American Redstart	-0.51 (-3.36, 4.62)	-1.23 (-4.30, 4.30)	3.91 (-0.15, 8.39)	0.05 (-0.18, 0.30)	-0.10 (-0.27, 0.10)	0.12 (-0.34, 0.63)	0.06 (-0.14, 0.23)	0.08 (-0.38, 0.56)	0.15 (-0.75, 0.88)
Black-and-white Warbler	-3.30 (-4.68, -1.80)*	-3.84 (-5.24, -2.39)*	4.19 (1.42, 8.37)*	0.10 (-0.10, 0.34)	-0.11 (-0.27, 0.07)	-0.21 (-0.61, 0.15)	0.04 (-0.20, 0.19)	-0.22 (-0.62, 0.15)	0.78 (0.28, 1.32)*
Warbling Vireo	-3.77 (-4.68, -2.80)*	-5.90 (-7.84, -4.45)*	5.16 (2.58, 7.98)*	0.03 (-0.18, 0.25)	-0.13 (-0.31, 0.03)	0.10 (-0.26, 0.51)	0.03 (-0.24, 0.18)	-0.37 (-0.89, 0.06)	-0.24 (-0.73, 0.22)
Pine Warbler	0.17 (-3.50, 4.95)	-1.12 (-4.65, 4.13)	2.56 (-2.39, 7.65)	0.04 (-0.22, 0.29)	-0.12 (-0.30, 0.07)	0.06 (-0.43, 0.60)	0.06 (-0.15, 0.25)	0.07 (-0.44, 0.61)	0.29 (-0.92, 1.33)

Rose-breasted Grosbeak	-3.27 (-8.42, 2.28)	-1.71 (-5.92, 3.74)	3.21 (-1.18, 7.88)	0.05 (-0.21, 0.32)	-0.11 (-0.30, 0.08)	-0.01 (-0.52, 0.52)	0.06 (-0.14, 0.25)	0.02 (-0.54, 0.60)	-0.25 (-1.44, 0.84)
Black-throated Green Warbler	-2.95 (-8.78, 2.81)	-2.96 (-7.35, 3.32)	2.93 (-1.42, 7.49)	0.01 (-0.26, 0.27)	-0.11 (-0.30, 0.07)	-0.03 (-0.53, 0.49)	0.07 (-0.12, 0.25)	0.11 (-0.44, 0.70)	0.09 (-1.05, 1.36)
<b>Interior community</b>	<b>-0.25 (-1.78, 1.27)</b>	<b>-1.85 (-3.58, -0.17)*</b>	<b>3.73 (2.31, 5.38)*</b>	<b>-0.02 (-0.36, 0.30)</b>	<b>-0.17 (-0.34, 0.01)</b>	<b>-0.12 (-0.30, 0.03)</b>	<b>0.28 (0.05, 0.51)*</b>	<b>0.46 (0.23, 0.69)*</b>	<b>0.38 (-0.16, 0.93)</b>
Acadian Flycatcher	1.88 (1.57, 2.22)*	0.21 (-0.22, 0.63)	3.45 (2.86, 4.08)*	-0.27 (-0.40, -0.13)*	-0.23 (-0.39, -0.08)*	-0.07 (-0.25, 0.11)	0.26 (0.01, 0.51)*	0.35 (0.11, 0.58)*	-0.13 (-0.34, 0.08)
Kentucky Warbler	1.62 (1.13, 2.17)*	-1.78 (-3.11, -0.86)*	4.54 (3.22, 6.38)*	0.48 (0.27, 0.71)*	-0.22 (-0.45, -0.02)*	-0.06 (-0.26, 0.20)	0.25 (-0.02, 0.54)	0.42 (0.14, 0.68)*	0.05 (-0.21, 0.32)
Wood Thrush	0.49 (0.14, 0.83)*	-0.97 (-1.39, -0.58)*	2.58 (1.93, 3.30)*	0.12 (-0.01, 0.26)	-0.21 (-0.37, -0.06)*	-0.03 (-0.20, 0.16)	0.24 (0.03, 0.44)*	0.40 (0.18, 0.60)*	-0.04 (-0.22, 0.14)
Scarlet Tanager	0.81 (0.33, 1.34)*	-0.20 (-0.82, 0.41)	1.49 (0.41, 2.70)*	-0.03 (-0.20, 0.15)	0.03 (-0.18, 0.27)	-0.22 (-0.48, -0.01)*	0.26 (-0.01, 0.52)	0.54 (0.31, 0.82)*	0.57 (0.34, 0.82)*
Ovenbird	-1.47 (-1.89, -1.06)*	-3.12 (-3.80, -2.54)*	4.18 (3.11, 5.42)*	-0.20 (-0.39, -0.01)*	-0.03 (-0.23, 0.22)	-0.17 (-0.41, 0.04)	0.53 (0.21, 0.93)*	0.71 (0.40, 1.07)*	1.02 (0.72, 1.33)*
Hooded Warbler	-1.61 (-2.00, -1.20)*	-3.95 (-4.86, -3.27)*	4.46 (3.36, 5.75)*	0.37 (0.19, 0.55)*	-0.23 (-0.45, -0.03)*	-0.20 (-0.46, 0.01)	0.41 (0.17, 0.72)*	0.56 (0.32, 0.81)*	1.12 (0.83, 1.45)*
Louisiana Waterthrush	-1.27 (-2.30, -0.01)*	-0.68 (-1.78, 0.69)	5.30 (2.80, 8.94)*	-0.25 (-0.60, 0.08)	-0.22 (-0.55, 0.04)	-0.14 (-0.47, 0.15)	0.21 (-0.16, 0.56)	0.30 (-0.15, 0.68)	-0.23 (-0.81, 0.33)
Worm-eating Warbler	-2.30 (-2.91, -1.67)*	-4.36 (-5.71, -3.42)*	3.88 (1.89, 6.56)*	-0.41 (-0.70, -0.13)*	-0.22 (-0.49, 0.00)	-0.10 (-0.36, 0.15)	0.08 (-0.23, 0.36)	0.45 (0.14, 0.75)*	0.71 (0.36, 1.09)*



**Figure 1.9.** Posterior means and 95% credible intervals for the effects of a) edge distance, b) amount of forest within 2 km, and c) log-transformed patch size on probability of occupancy for breeding forest bird communities. Species were divided into three forest habitat groups (interior specialist, forest generalist, or edge specialist), and the mean effect of the covariate on members of each group was estimated along with individual effects. Within each habitat group, species are listed from most common (top) to least common, or equivalently, from most influential on the group mean estimate, to least. Note that all covariates were standardized with a mean of 0 and standard deviation of 1 prior to model fitting.





**Figure 1.10.** Predicted richness ( $\pm$  95% credible intervals) of breeding forest birds occupying a 50 m radius forest plot varies as a function of forest patch size (left) local forest cover (right), and habitat group. Predicted richness values were calculated from each of 6,000 draws from the posterior distributions of a community occupancy model, and represent the sum of the predicted occupancy probabilities of 52 species when all other local and landscape variables are held constant at their mean.

Results from these analyses yielded no support for the fragmentation threshold hypothesis, which suggests that fragmentation should have greater effects on species distributions when habitat amount drops below approximately 30% (Andren 1994; Fahrig 2003). The minimum habitat amount for any of our sample points was approximately 11%, and only 20 of our points were surrounded by less than 30% forest cover, and thus, it is plausible that we simply did not have enough data for points below this threshold to detect a significant interaction effect. Similarly, we found little support for Fahrig's (2013) habitat amount hypothesis. In contrast to these well-established ideas, our results unequivocally demonstrate that patch size per se has a significant influence on the distribution pattern of many species. Moreover, the relative impact of patch size is above and beyond the amount of forest it contributes to the local landscape. Finally, while species richness varies little with patch size, community composition does change in predictable ways.

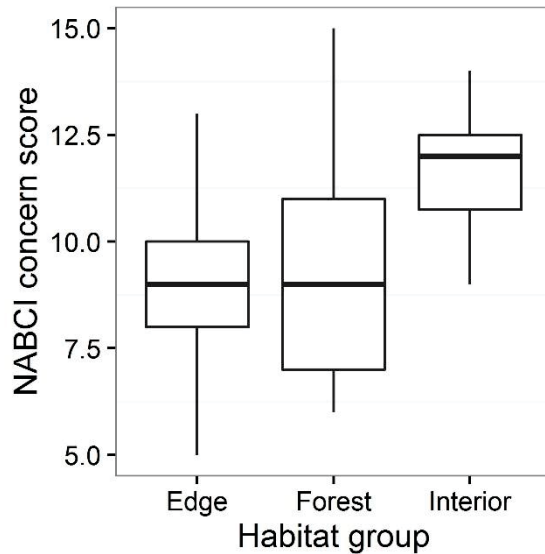
Our results suggest that the patch size effects are likely driven by patch geometry rather than the colonization and extinction dynamics. Although we did see a high degree of positive correlation between initial occupancy rates and colonization rates, and negative correlation between initial occupancy and extinction rates, neither process was influenced by patch size for most species. Moreover, we did not find any evidence that total species richness increased with increasing patch size. Rather, we found that the average patch size effect on occupancy was significantly positive for species richness of interior specialists, significantly negative for edge specialists, and approximately zero for forest generalists (Fig. 1.19). Bender et al. (1998) identified a similar pattern in their review of patch size effects on animal densities and pointed out that the amount of habitable area is severely overestimated for interior species at low patch sizes, and for edge species at large patch sizes. Our results may have been driven by a similar mechanism, because the size of a contiguous habitable interior patch would increase with forest patch size, while the concentration of edge habitat would actually be greatest in small patches.



Contrary to the results from other studies (Andren 1994, McGarigal and McComb 1995, Trzcinski et al. 1999, McGarigal and Cushman 2002, Fahrig 2003, 2013, 2017, Turner 2005), we did not find a reduction in the amount of forest cover to be overwhelmingly detrimental to bird distributions in our study area. In fact, we found the opposite pattern for many species, particularly cavity nesters (Fig. 1.19). We interpret this as an indication that availability of cavity trees is somehow inversely related with forest cover in our study region. Tree mortality tends to be greater near forest edges (e.g., Chen et al. 1992, Esseen 1994), and it is possible that landscapes with lower forest cover in our study tended to have greater edge-to-area ratios, though this is admittedly speculative. Regardless of the mechanism, failure to account for the distribution of cavity trees likely meant that forest cover was a poor measure of habitat amount, even for many of our forest generalist species.

There is widespread consensus that testing the predictions of island biogeography theory, metapopulation theory, or the relative effects of patch size and habitat amount requires defining habitat uniquely for each species (Betts et al. 2014, Hanski 2015) or species group (Gonzalez et al. 2010, Fahrig 2013). Because both our patch size and habitat amount measures were likely imprecise for most species, our study probably does not constitute a rigorous test of these controversial topics. Unfortunately, designing multi-species studies that both account for idiosyncrasies in habitat requirements (Fahrig 2013, Betts et al. 2014, Hanski 2015), and minimize correlation between composition and configuration variables (Fahrig 2003, Hadley and Betts 2016) for all species would require an extraordinary financial and logistical effort. The spatial distribution of sampling points may need to be unique for each species, and even then, it may be unclear how to define patch boundaries (Betts et al. 2006, 2007, 2014). Thus, while we certainly acknowledge that these fine scale distinctions are critical for testing theory, our results are quite clear on a practical level: forest patch size per se does influence the distribution of many species, particularly interior and edge specialists.

Fahrig (2017) recently noted that the vast majority (76%) of significant fragmentation effects found in the literature are positive (Fahrig 2017). That is, the distributions of individual species are far more likely to increase, rather than decrease, with fragmentation. While it may be arguable whether focal patch studies such as ours truly test fragmentation effects (McGarigal and Cushman 2002, Fahrig 2003, 2017), our results notably contrast with one of Fahrig's (2017) main conclusions that "there is no justification for assigning lower conservation value to a small patch than to an equivalent area within a large patch..." Occupancy probability was not only higher for interior species in large forest patches, but members of this group also tend to be of significantly greater conservation concern than forest edge ( $t = 2.92$ ,  $p = 0.005$ ) or generalist ( $t = 2.81$ ,  $p = 0.007$ ) species (NABCI 2016; Fig. 1.11). Indeed, the ratio of interior to edge specialists in our study region may help explain the overwhelming majority of positive fragmentation effects; if species that prefer edge habitat are simply more common, one would expect to find positive effects of reduced patch size more often. Regardless of the mechanism, our results clearly demonstrate that larger forest patches do, in fact, have greater conservation value for many species.



**Figure 1.11.** The distribution of conservation concern scores for 52 species classified as edge specialists, forest generalists, or interior specialists (NABCI 2016). Interior specialists, which tend to be positively associated with forest patch size, also tend to be of greatest conservation concern.

Many have argued that there is no value in managing habitat patches because: larger patches do not tend to have higher species richness, as predicted by Island Biogeography Theory, (e.g., Fahrig 2013, Mendenhall et al. 2014); patch boundaries typically do not contain demographically distinct units as required in a metapopulation framework (McIntyre and Barrett 1992, Wiens 1994, Baguette 2004, Manning et al. 2004, Fischer and Lindenmayer 2006, Fahrig 2013); and the amount of habitat is vastly more important than the size of any given patch (Andren 1994, McGarigal and McComb 1995, Trzcinski et al. 1999, McGarigal and Cushman 2002, Fahrig 2003, 2013, 2017, Turner 2005). Yet the fact of the matter is that some species require large forest patches in order to have any habitat available to them at all. We acknowledge that a conservation strategy focused on maintaining

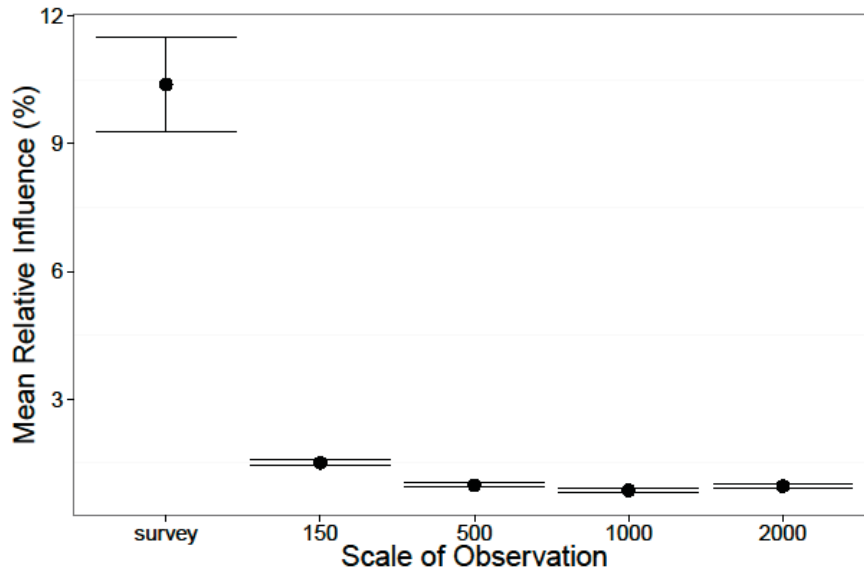
large forest patches will absolutely not be beneficial for all or even most species (Fahrig 2017); however, given that core forest area has become extremely scarce worldwide (Haddad et al. 2015), protecting large forest patches may, in fact, be more immediately pressing in our study region and in many other parts of the world (e.g., Robinson et al. 1995, Gibson et al. 2013).

### Species Distribution Models for Common Breeding Species

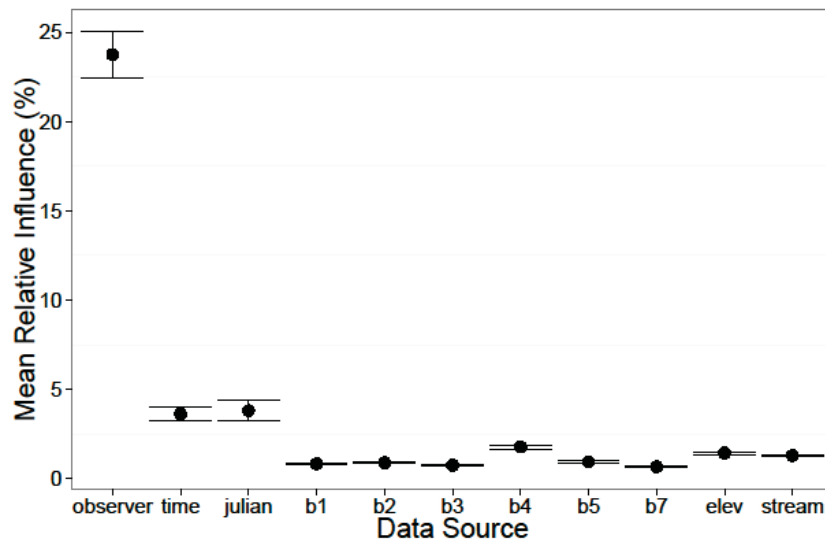
Prediction success based on validation datasets was unfortunately lower than we would have liked. AUC values for the 30 species ranged from a low of 0.63 to a high of 0.86, with a mean of only 0.72 (Table 1.14). Only 18 species had BRTs with an AUC of  $\geq 0.7$ , and thus SDMs were only constructed for those species. Perhaps a large part of the problem stemmed from the fact that survey-level covariates (observer, time of day, and Julian date) had by far the greatest relative influence on observed distribution patterns in models for all species (Figures 1.12 and 1.13). This indicates that observed distribution patterns are heavily influenced by imperfect detection, which may hinder the ability to discern true relationships with habitat features (Gu and Swihart 2004). Habitat features measured at the finest spatial scales (150 m and 500 m) tended to have the greatest influence on observed distribution patterns (Figure 1.12). In addition, Landsat TM band 4 metrics tended to have the strongest influence on the responses, followed by elevation and stream distance (Figure 1.13). However, all measured explanatory variables had non-trivial influence the distributions of one or more species. Figure 1.14 depicts an image of the SDM developed for Wood Thrush, and all SDMs will be provided to the DoD as geo-rectified image (GeoTiff).

**Table 1.14** Area under the receiver operating characteristic curve (AUC) for boosted regression tree (BRT) models fit for 30 common bird species in southern Indiana. An AUC of greater than 0.7 indicates that the model has useful discriminatory power (Hosmer and Lemeshow 2000), and thus species distribution models were constructed from the BRTs for only the first 18 species listed.

Species	Validation AUC
Ovenbird	0.86
Hooded Warbler	0.81
Common Yellowthroat	0.79
Yellow-breasted Chat	0.79
Acadian Flycatcher	0.78
Northern Cardinal	0.77
White-eyed Vireo	0.76
Blue-gray Gnatcatcher	0.75
Northern Parula	0.75
Indigo Bunting	0.74
Wood Thrush	0.74
Red-eyed Vireo	0.73
Gray Catbird	0.72
Carolina Wren	0.72
Red-bellied Woodpecker	0.72
Eastern Towhee	0.72
Yellow-throated Warbler	0.70
Scarlet Tanager	0.70
Kentucky Warbler	0.69
Great-crested Flycatcher	0.69
Blue Jay	0.68
White-breasted Nuthatch	0.68
Eastern-wood Pewee	0.67
Carolina Chickadee	0.67
Yellow-throated Vireo	0.66
Tufted Titmouse	0.66
Hairy Woodpecker	0.66
Downy Woodpecker	0.65
Summer Tanager	0.65
Northern Flicker	0.63



**Figure 1.12** Mean ( $\pm$  SE) relative influence of explanatory covariates on species distributions across all species grouped by scale of measurement. The survey-level explanatory variables (observer, time of day, and Julian date) were measured every time a site was visited. All other explanatory variables (mean and SD of Landsat TM bands, stream distance, and elevation) were measured at 4 spatial scales (150 m, 500 m, 1000 m, and 2000 m).

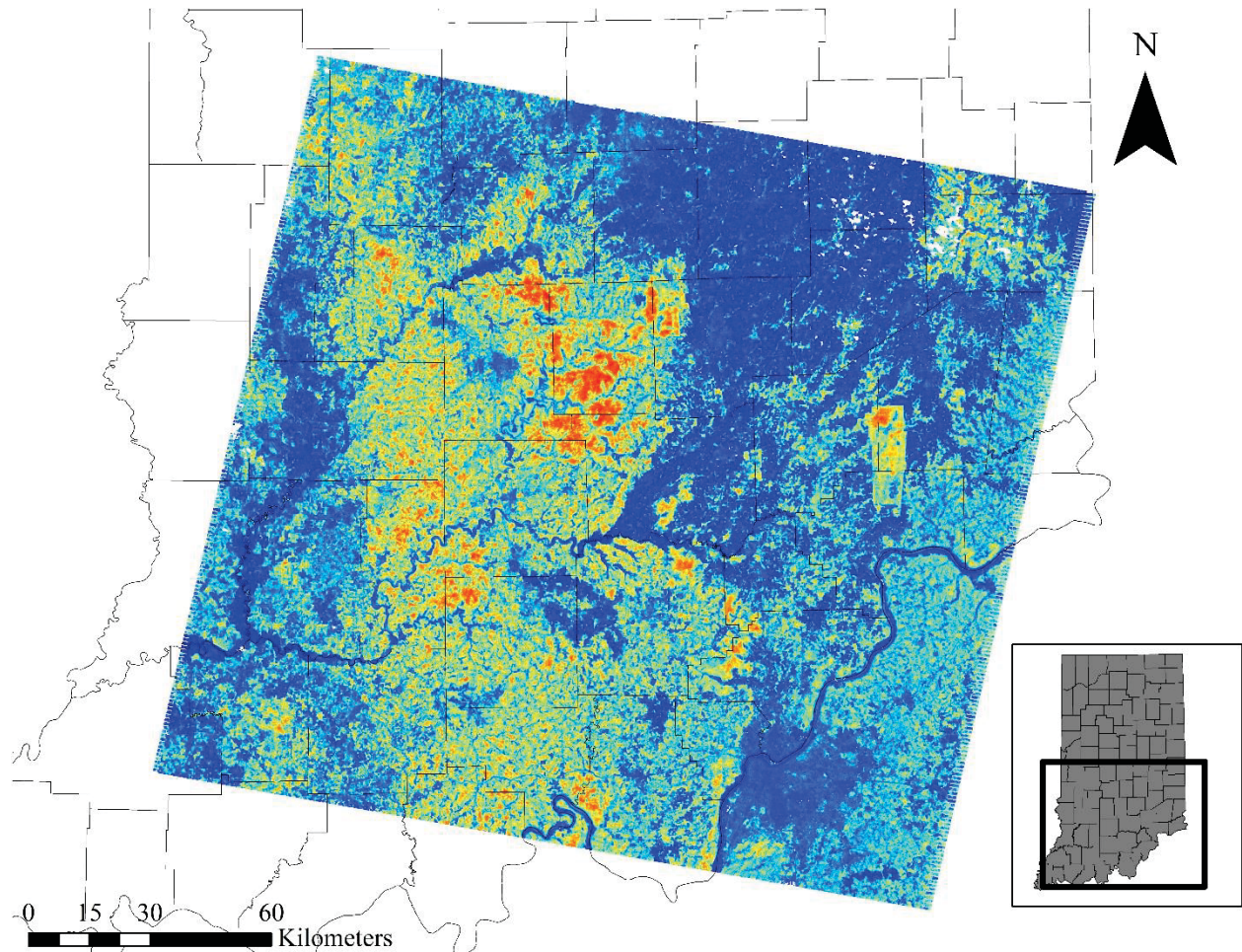


**Figure 1.13** Mean ( $\pm$  SE) relative influence of explanatory covariates on species distributions across all species grouped by data source. The survey-level explanatory variables (observer, time of day, and Julian date) were measured every time a site was visited. All other explanatory variables (mean and SD of Landsat TM bands, stream distance, and elevation) were measured at 4 spatial scales (150 m, 500 m, 1000 m, and 2000 m).

## Conclusions and Implications for Future Research

Our results can be extrapolated to provide a number of useful recommendations to DoD wildlife managers. First, when interest is in quantifying population dynamics, identifying source-sink habitats, or population trends from samples of unmarked animals, there are a few key

rules to follow. First, when temporary emigration from sample sites is not of concern, studies may use distance (Buckland *et al.* 2001; Royle *et al.* 2004), time of detection (Farnsworth *et al.* 2002; Alldredge *et al.* 2007), double-observer (Nichols *et al.* 2000; Alldredge *et al.* 2006) or repeated sampling (MacKenzie *et al.* 2002; Royle & Nichols 2003; Royle 2004) methods to quantify occupancy or abundance patterns while accounting for imperfect detection. In situations where TE is possible, however, repeated sampling protocols are essential, and samples within primary periods should be spaced such that TE occurs randomly and independently on each visit, but rates population dynamics are negligible. Only then can managers generate accurate estimates of distributional changes.



**Figure 1.14** An image of the species distribution model (SDM) developed for Wood Thrush in southern Indiana based on breeding season point count data.

Secondly, while our results indicated that colonization and extinction rates were not influenced by fragmentation for most bird species utilizing DoD properties and surrounding areas, we were only able to model these rates between breeding seasons. Species that migrate obviously tend to be much more mobile between breeding seasons, and thus these results may not reflect how fragmentation influences dispersal within a breeding season. Juveniles prospecting for future breeding sites in late summer may be particularly limited by fragmentation, and thus future work should focus on estimating within-season dynamic rates, while appropriately accounting for the effects of TE.



Finally, while our results may be limited by the fact that habitat amount and patch size were not measured accurately for all species, they unequivocally demonstrate that maintaining large forest patches is critical for supporting interior specialists, which tend to be of greatest conservation concern. As a next step, we intend to utilize our SDMs to quantify patch size and habitat amount on a species-by-species basis. We will then compare distribution models for the same species using the generic and species-specific quantifications of landscape metrics. This will allow us to test the hypotheses that including species-specific landscape metrics in these models will: 1) increase the amount of variability explained by those landscape features, thereby increasing the number of species deemed fragmentation sensitive; and 2) augment the relative importance of those landscape features on distributions of each species, indicating a greater degree of sensitivity to fragmentation than estimated using generic measurements. If both of these hypotheses are supported, we will have strong evidence that the lack of congruency between landscape theory and empirical data has been driven, in part, by poor landscape measurements.

### Literature Cited

- Allredge, M.W., Pollock, K.H., Simons, T.R., Collazo, J.A. & Shriner, S.A. (2007) Time-of-detection method for estimating abundance from point-count surveys. *The Auk*, **124**, 653–664.
- Allredge, M.W., Pollock, K.H. & Simons, T.R. (2006) Estimating detection probabilities from multiple-observer point counts. *The Auk*, **123**, 1172–1182.
- Andren, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat : a review. *Oikos*, **71**, 355–366.
- Austin, M.P. (1985) Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics*, **16**, 39–61.
- Baguette, M. (2004) The classical metapopulation theory and the real, natural world: a critical appraisal. *Basic and Applied Ecology*, **5**, 213–224.
- Bender, D.J., Contreras, T.A. & Fahrig, L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology*, **79**, 517–533.
- Betts, M.G., Fahrig, L., Hadley, A.S., Halstead, K.E., Bowman, J., Robinson, W.D., Wiens, J.A. & Lindenmayer, D.B. (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. *Ecography*, **37**, 517–527.
- Betts, M.G., Forbes, G.J., Diamond, A.W. & Taylor, P.D. (2006) Independent effects of fragmentation on forest songbirds: an organism-based approach. *Ecological Applications*, **16**, 1076–1089.
- Betts, M.G., Forbes, G.J. & Diamond, A.W. (2007) Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology*, **21**, 1046–58.
- Betts, M.G., Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. (2008) Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. *Ecography*, **31**, 592–600.
- Blandon, A.C., Perelman, S.B., Ramirez, M., Lopez, A., Javier, O. & Robbins, C.S. (2016) Temporal bird community dynamics are strongly affected by landscape fragmentation in a Central American tropical forest region. *Biodiversity Conservation*, **25**, 311–330.
- Bried, J.T., & Pellet, J. (2012) Optimal design of butterfly occupancy surveys and testing if occupancy converts to abundance for sparse populations. *Journal of Insect Conservation*, **16**, 489–499.
- Breiman, L. (2001) Statistical modeling: the two cultures. *Statistical Science*, **16**, 199–215.

- Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., & Thomas, L. (2001) *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, New York.
- Carrara, E., Arroyo-Rodriguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S.M., & Fahrig, L. (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biological Conservation*, **184**, 117-126.
- Chandler, R.B., Royle, J.A. & King, D.I. (2011) Inference about density and temporary emigration in unmarked populations. *Ecology*, **92**, 1429–1435.
- Chen, J., Franklin, J.F. & Spies, T.A. (1992) Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecological Applications*, **2**, 387-396.
- Cook, W.M., Lane, K.T., Foster, B.L. & Hold, R.D. (2002) Island theory, matrix effects and species richness patterns in habitat fragments. *Ecology Letters*, **5**, 619-623.
- Dail, D. & Madsen, L. (2013) Estimating open population site occupancy from presence-absence data lacking the robust design. *Biometrics*, **69**, 146-156.
- Dail, D. & Madsen, L. (2011) Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, **67**, 577–587.
- Dorazio, R.M. & Royle, J.A. (2005) Estimating size and composition of biological communities by modeling the occurrences of species. *Journal of the American Statistical Association*, **100**, 389-398.
- Efford, M.G. & Dawson, D.K. (2012) Occupancy in continuous habitat. *Ecosphere*, **3**, 32.
- Elith, J., Graham, C.H., Anderson, R.P., Miroslav, D., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Peterson, A.T., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberon, J., Williams, S., Wisz, M.S. & Zimmerman, N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.
- Elith, J., Leathwick, J.R. & Hastie, T. (2008) A working guide to boosted regression trees. *Journal of Animal Ecology*, **77**, 802–813.
- Emlen, J.T. (1967) A rapid method for estimating arboreal canopy cover. *Ecology*, **48**, 158–160.
- Esseen, P.A. (1994) Tree mortality patterns after experimental fragmentation of an old-growth conifer forest. *Biological Conservation*, **68**, 19-28.
- Fahrig, L. (2003) Effects of Habitat Fragmentation on Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 487–515.
- Fahrig, L. (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis (ed K Triantis). *Journal of Biogeography*, 1–15.
- Fahrig, L. (2017) Ecological responses to habitat fragmentation per se. *Annual Review of Ecology, Evolution, and Systematics*, **48**.
- Farnsworth, G.L., Pollock, K.H., Nichols, J.D., Simons, T.R., Hines, J.E. & Sauer, J.R. (2002) A removal model for estimating detection probabilities from point-count surveys. *The Auk*, **119**, 414–425.
- Fischer, J. & Lindenmayer, D.B. (2006) Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. *Oikos*, **112**, 473–480.
- Fiske, I.J., & Chandler, R.B. (2011) unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software*, **43**, 1-23.



- Friedman, J.H. (2001) Greedy function approximation: a gradient boosting machine. *Annals of Statistics*, **29**, 1189-1232.
- Friedman, J.H., Hastie, T. & Tibshirani, R. (2000) Additive logistic regression: a statistical view of boosting. *Annals of Statistics*, **28**, 337-407.
- Gelman, A., Carlin, J.B., Sterns, H.S., & Rubin, D.B. 2004. *Bayesian Data Analysis*. Chapman and Hall, Boca Raton, Florida, USA.
- Gelman A. & Hill J. (2007) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, New York.
- Gibson, L., Lynam, A.J., Bradshaw, C.J.A., He, F., Bickford, D.P., Woodruff, D.S., Bumrungsri, S. & Laurance, W.F. (2013) Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science*, **341**, 1508-1510.
- Godefroid, S. & Koedam, N. (2003) How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Global Ecology and Biogeography*, **12**, 287-298.
- Gonzalez, M., Ladet, S., Deconchat, M., Cabanettes, A., Alard, D. & Balent G. (2010) Relative contribution of edge and interior zones to patch size effect on species richness: an example for woody plants. *Forest Ecology and Management*, **259**, 266-274.
- Grinnell, J. (1917) The niche-relationships of the California Thrasher. *Auk*, **34**, 427-433.
- Gu, W. & Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, **116**, 195-203.
- Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A. O., Orrock, J.L., Song, D. & Townshend, J.R. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, **1**, e1500052.
- Hadley, A.S. & Betts, M.G. (2016) Refocusing habitat fragmentation research using lessons from the last decade. *Current Landscape Ecology Reports*.
- Haila, Y. (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications*, **12**, 321–334.
- Hanski, I. (2015) Habitat fragmentation and species richness. *Journal of Biogeography*, **42**, 989-994.
- Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.
- Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.
- Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2016) *dismo: Species Distribution Modeling*. R package version 1.0-12. <http://CRAN.R-project.org/package=dismo>.
- Homer, C.G., Dewitz, J.A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulstan, J., Herold, N.D., Wickham, J.D. & Megown, K. (2015) Completion of the 2011 National Land Cover Database for the conterminous United States – representing a decade of land cover change information. *Photogrammetric Engineering and Remote Sensing*, **81**, 345-354.
- Hosmer, D.W. & Lemeshow, S. (2000) *Applied Logistic Regression*, 2<sup>nd</sup> edition. John Wiley and Sons, New York, USA.
- Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415-427.
- Iida, S. & Nakashizuka, T. (1995) Forest fragmentation and its influence on plant species diversity in sub-urban coppice forest in Japan. *Forest Ecology and Management*, **73**, 197-210.

- Iknayan, K.J., Tingley, M.W., Furnas, B.J. & Bessinger, S.R. (2014) Detecting diversity: emerging methods to estimate species diversity. *Trends in Ecology and Evolution*, **29**, 97-106.
- Kellner, K. (2016) *jagsUI: A Wrapper Around 'rjags' to Streamline 'JAGS' Analyses*, R package version 1.44. <https://github.com/kenkellner/jagsUI>.
- Kendall, W.L., Hines, J.E., Nichols, J.D. & Grant, E.H.C. (2013) Relaxing the closure assumption in occupancy models: staggered arrival and departure times. *Ecology*, **94**, 610–617.
- Kendall, W.L. (1999) Robustness of closed capture-recapture methods to violations of the closure assumption. *Ecology*, **80**, 2517-2525.
- Kendall, W.L., Nichols, J.D. & Hines, J.E. (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, **78**, 563–578.
- Kerr, J.T. & Ostrovsky, M. (2003) From space to species: ecological applications for remote sensing. *Trends in Ecology and Evolution*, **18**, 299-305.
- Kery, M. & Royle, J.A. (2008) Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, **45**, 589-598.
- Kery, M. & Royle, J.A. (2016) *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS*. Elsevier, Inc., London, UK.
- Khimoun, A., Eraud, C., Ollivier, A., Arnoux, E., Rocheteau, V., Bely, M., Lefol, E., Delpuech, M., Carpentier, M.-L., Leblond, G., Levesque, A., Charbonnel, A., Faivre, B. & Garnier, S. (2016) Habitat specialization predicts genetic response to fragmentation in tropical birds. *Molecular Ecology*, **25**, 3831-3844.
- Kolb, A. & Diekmann, M. (2004) Effects of environment, habitat configuration and forest continuity on the distribution of forest plant species. *Journal of Vegetation Science*, **15**, 199-208.
- Lande, R. (1987) Extinction thresholds in demographic models of territorial populations. *American Naturalist*, **130**, 624-635.
- Lawesson, J.E., de Blust, G., Grashof, C., Firbank, L., Honnay, O., Hermy, M., Hobitz, P. & Jensen, L.M. (1998) Species diversity and area-relationships in Danish beech forests. *Forest Ecology and Management*, **106**, 235-245.
- Levins, R. (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.
- Lindenmayer, D.B. & Fischer, J. (2007) Tackling the habitat fragmentation panchreston. *Trends in Ecology & Evolution*, **22**, 127–32.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373-387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ, USA.
- MacKenzie, D.I. (2005) What are the issues with presence-absence data for wildlife managers? *Journal of Wildlife Management*, **69**, 849–860.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.
- MacKenzie, D.I. & Royle, J.A. (2005) Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, **42**, 1105–1114.

- Manning, A.D., Lindenmayer, D.B. & Nix, H.A. (2004) Continua and Umwelt: novel perspectives on viewing landscapes. *Oikos*, **104**, 621–628.
- McClure, C.J.W. & Hill, G.E. (2012) Dynamic versus static occupancy: How stable are habitat associations through a breeding season? *Ecosphere*, **3**, 1–13.
- McGarigal, K. & Cushman, S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation. *Ecological Applications*, **12**, 335–345.
- McGarigal, K. & McComb, W.C. (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs*, **65**, 235–260.
- McIntyre, S. & Barrett, G.W. (1992) Habitat variegation, an alternative to fragmentation. *Conservation Biology*, **6**, 146–147.
- McIntyre, S. & Hobbs, R.J. (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. *Conservation Biology*, **13**, 1282–1292.
- Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A. & Daily, G.C. (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature*, **509**, 213–217.
- Nichols, J.D., Hines, J.E., Sauer, J.R., Fallon, F.W., Fallon, J.E. & Heglund, P.J. (2000) A double-observer approach for estimating detection probability and abundance from point counts. *The Auk*, **117**, 393–408.
- Nichols, J.D., Thomas, L. & Conn, P.B. (2009) Inferences about landbird abundance from count data: recent advances and future directions. *Modeling Demographic Processes in Marked Populations* (eds D.L. Thomson, E.G. Cooch & M.J. Conroy), pp. 201–235. Springer Science+Business Media, LLC, New York.
- North American Bird Conservation Initiative (2016) *The State of North America's Birds 2016*. Environment and Climate Change Canada, Ottawa, Ontario.
- Noss, R.F. (1991) Landscape connectivity: different functions at different scales. *Landscape Linkages and Biodiversity* (ed W.E. Hudson), pp. 27–39. Island Press, Washington DC, USA.
- O'Donnell, K.M., Thompson, F.R. & Semlitsch, R.D. (2015) Partitioning detectability components in populations subject to within-season temporary emigration using binomial mixture models. *Plos One*, **10**, e0117216.
- Otto, C.R.V., Bailey, L.L. & Roloff, G.J. (2013) Improving species occupancy estimation when sampling violates the closure assumption. *Ecography*, **36**, 1299–1309.
- Otto, C.R.V., & Roloff, G.J. (2012) Songbird response to green-tree retention prescriptions in clearcut forests. *Forest Ecology and Management*, **284**, 241–250.
- Pimm, S.L. & Raven, P. (2000) Extinction by numbers. *Nature*, **403**, 843–845.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science*, **269**, 347–350.
- Plummer, M. (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.
- Pollock, K.H. (1982) A capture-recapture design robust to unequal probability of capture. *Journal of Wildlife Management*, **46**, 752–757.
- Prugh, L.R., Hodges, K.E., Sinclair, A.R.E. & Brashares, J.S. (2008) Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences*, **105**, 20770–20775.
- Puttker, T., Bueno, A.A., de Barros, C.d.S., Sommer, S. & Pardini, R. (2013) Habitat specialization interacts with habitat amount to determine dispersal success of rodents in fragmented landscapes. *Journal of Mammalogy*, **94**, 714–726.

- Riddle, J.D., Stanislav, S.J., Pollock, K.H., Moorman, C.E. & Perkins, F.S. (2010) Separating components of the detection process with combined methods: an example with northern bobwhite. *Journal of Wildlife Management*, **74**, 1319–1325.
- Ridgeway, G. with contributions from others (2015) *gbm: Generalized Boosted Regression Models*, R package version 2.1.1. <http://CRAN.R-project.org/package=gbm>.
- Robinson, S.K., Thompson, F.R., Donovan, T.M., Whitehead, D.R. & Faaborg, J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.
- Rodewald, P. (2015) *The Birds of North America*: <https://birdsna.org>. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
- Rota, C.T., Fletcher Jr, R.J., Dorazio, R.M. & Betts, M.G. (2009) Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, **46**, 1173–1181.
- Royle, J.A. (2004) N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, **60**, 108–115.
- Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.
- Ruiz-Gutierrez, V., Zipkin, E.F. & Dhondt, A.A. (2010) Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. *Journal of Applied Ecology*, **47**, 621–630.
- Samu, F., Csontos, P. & Szinetar, C. (2008) From multi-criteria approach to simple protocol: assessing habitat patches for conservation value using species rarity. *Biological Conservation*, **141**, 1310–1320.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.
- Schmidt, J.H., McIntyre, C.L. & MacCluskie, M.C. (2013) Accounting for incomplete detection: What are we estimating and how might it affect long-term passerine monitoring programs? *Biological Conservation*, **160**, 130–139.
- Self, S.G. & Liang, K. (1987) Asymptotic properties of maximum likelihood estimators and likelihood ratio tests under nonstandard conditions. *Journal of the American Statistical Association*, **82**, 605–610.
- Shirley, S.M., Yang, Z., Hutchinson, R.A., Alexander, J.D., McGarigal, K. & Betts, M.G. (2013) Species distribution modelling for the people: unclassified landsat TM imagery predicts bird occurrence at fine resolutions. *Diversity and Distributions*, 1–12.
- Sollmann, R., Gardner, B., Chandler, R.B., Royle, J.A. & Sillett, T.S. (2015) An open-population hierarchical distance sampling model. *Ecology*, **96**, 325–331.
- Spendelov, J.A., & Nichols, J.D. (1989) Annual survival rates of breeding adult Roseate Terns (*Sterna dougalii*). *The Auk*, **106**, 367–374.
- Swihart, R.K., & Slade, N.A. (1985) Testing for independence of observations in animal movements. *Ecology*, **66**, 1176–1184.
- Tingley, M.W. & Beissinger, S.R. (2013) Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology*, **94**, 598–609.
- Trzcinski, K.M., Fahrig, L. & Merriam, G. (1999) Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecological Applications*, **9**, 586–593.
- Turner, M. (2005) Landscape ecology: what is the state of the science? *Annual Reviews of Ecology, Evolution and Systematics*, **36**, 319–344.

- Wiens, J.A. (1994) Habitat fragmentation: island vs landscape perspectives on bird conservation. *Ibis*, **137**, S97–S104.
- Wilcove, D.S., McLellan, C.H. \* Dobson, A.P. (1986) Habitat fragmentation in the temperate zone. *Conservation Biology* (ed M.E. Soule), pp. 237-256. Sinauer Associates, Sunderland, MA, USA.
- With, K.A. & King A.W. (1999) Extinction thresholds for species in fractal landscapes. *Conservation Biology*, **13**, 314-326.
- Yamura, Y., Connor, E.F., Royle, J.A., Itoh, K., Sato, K., Taki, H. & Mishima, Y. (2016) Estimating species-area relationships by modeling abundance and frequency subject to incomplete sampling. *Ecology and Evolution*, **6**, 4836-4848.
- Zipkin, E.F., DeWan, A. & Royle, J.A. (2009) Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology*, **46**, 815-822.



## **Chapter 2- Estimating vital rates of Wood thrush at Monitoring Avian Productivity and Survivorship (MAPS) Stations**

### **Abstract**

The Monitoring Avian Productivity and Survivorship program (MAPS) is a cooperative mist-netting and bird-banding program that has been implemented at hundreds of sites (stations) across North America each summer for more than 20 years. MAPS has proven an attractive option for land managers charged with monitoring landbirds because demographic data for multiple species can be gathered with relatively modest effort. Here, we summarize data and results from MAPS stations operated at 18 sites in southern Indiana between 2011-2014 (eight of these stations were also operated in years prior to 2011). The 18 stations were arranged within three locations (i.e., clusters) of 6 stations each. Each location was represented by a contiguous landholding, including: 1) Naval Support Activity Crane (CRANE), 2) NSA Crane and Hoosier National Forest (IDNR), and 3) Big Oaks National Wildlife Refuge (BONWR). Twelve of these stations were also included within a larger study that incorporated more intensive monitoring methods to study Wood Thrush demography and population dynamics. We assessed spatial variation in vital rates and provide estimates of an index of post-fledging productivity (predicted capture ratio of young to adult birds) and adult apparent survival probability for Wood Thrush from MAPS data at the scale of stations to provide a point of comparison with the more intensive demographic study. We found support for spatial variation in productivity at both location and station scales. At location scale, productivity was lowest at IDNR (0.15; 95% CI: 0.11, 0.17) and higher at BONWR (0.23; 95% CI: 0.17, 0.30) and CRANE (0.27; 95% CI: 0.19, 0.38). Productivity did not correspond closely to fecundity values estimated for the 12 intensive demographic monitoring sites; however, we found that productivity was positively related to forest cover within 2 km of at these sites, suggesting that MAPS may accurately reflect productivity and habitat conditions at larger landscape scales. Similar to the pattern of productivity, adult apparent survival was also relatively low at IDNR (0.50 [95% CI: 0.38, 0.62]) compared to the other two locations (0.60 [95% CI: 0.41, 0.75] at CRANE; 0.65 [95% CI: 0.50, 0.77] at BONWR). Overall, these data provide not only a useful point of comparison for the intensive demographic monitoring efforts, but they also represent a valuable contribution to the larger regional and continental MAPS program.

### **Objective**

Here, we use MAPS monitoring, constant effort mist-netting, to characterize the contribution of key vital rates (survival and fecundity) to population growth. This modest-effort approach is desirable because vital rate data can be collected across a suite of forest breeding species. The two primary objectives were to: 1) Examine MAPS as a tool to characterize demography (survival and fecundity) for a species of concern on DoD properties, the Wood thrush and 2) identify the local and landscape drivers of spatial variation in Wood thrush productivity on DoD installations and more broadly across southern Indiana. A review of the pros and cons of each methodological approach and their utility for assessing changes in population growth is covered in Chapter 4.

### **Background**

The Monitoring Avian Productivity and Survivorship program (MAPS) is a cooperative mist-netting and bird-banding program established by The Institute for Bird Populations (IBP) and cooperators in 1989. The current MAPS field protocol was standardized in 1992 and since that

time > 2 million capture records have been registered at > 1200 monitoring stations across North America. The principal aim of MAPS since its initiation has been to provide a means of estimating and monitoring vital rates of landbirds across broad spatial scales via standardized replicated mist-netting and bird banding (DeSante and Kaschube 2009). MAPS has proven an attractive option for land managers charged with monitoring landbirds because demographic data for multiple species can be gathered with relatively modest effort compared to more intensive demographic monitoring methods (Ralph et al. 1993). Statistical models applied to MAPS data have provided basic estimates of demographic parameters for > 150 landbird species (Albert et al. 2016) and have provided insights into spatial patterns in vital rates (Saracco et al. 2010; 2012), environmental drivers of vital rates (Nott et al. 2002; LaManna et al. 2012; George et al. 2015) and demographic causes of population change (Saracco et al. 2008; Rushing et al. 2016; Ryu et al. 2016).

Despite the broad interest and effort invested in MAPS and important insights provided by the program at regional and range-wide scales (e.g., Saracco et al. 2008; Rushing et al. 2016), there have been few assessments of the protocol's ability to provide accurate demographic information for local landscapes (Bart et al. 1999; Ralph and Dunn 2004). IBP, in collaboration with colleagues at the Smithsonian Migratory Bird Center (SMBC) and Oregon State University (OSU), operated 18 MAPS stations in southern Indiana between 2011 and 2014. Here, we summarize species breeding status, effort, and captures at these stations and provide estimates of an index of post-fledging productivity and adult apparent survival probability for Wood Thrush (*Hylocichla mustelina*). Twelve of the 18 MAPS stations were also the focus of intensive demographic monitoring efforts for Wood Thrush, providing an important test of how demographic estimates derived from MAPS data relates to similar parameters estimated from the more intensive monitoring techniques.

## Methods

### Study Areas

We established 18 MAPS stations, arranged in clusters of six stations at each of three locations in southern Indiana in the summers of 2011-2014. The three locations were at Naval Support Activity Crane (CRANE), Big Oaks National Wildlife Refuge (BONWR), and NSA Crane and Hoosier National Forest (IDNR). Five stations at CRANE and three stations at BONWR had been previously operated during some or all of 1994-2008 as part of the continent-wide MAPS program, whereas one station at CRANE, three stations at BONWR, and the six stations at IDNR were newly established in 2011 (Table 2.1). Each station consisted of a sampling area of about 20 ha. Within the central 8 ha of each station, 10 12-m long, 30-mm mesh, 4-tier nylon mist nets were erected at fixed net sites.

**Table 2.1** Monitoring Avian Productivity and Survivorship (MAPS) stations operated in southern Indiana in 2011-2014, history of operation prior to the present study, and total number of years operated as part of the MAPS program.

Region <sup>a</sup>	Station	Code	Latitude	Longitude	Elevation (m)	Years operated < 2011	No. years
CRANE	Area 14	AR14	38.84083	-86.7947	198	1994-2002, 2004-2008	18
CRANE	East Boggs	EABO	38.79417	-86.8356	152	1994-2002, 2004-2008	18
CRANE	First Creek	FIRS	38.87139	-86.9025	162	1994-2002, 2004-2008	18
CRANE	Seedtick Creek	SEED	38.75972	-86.8847	149	1994-2002, 2004-2008	18
CRANE	Sulphur Creek	SULP	38.88528	-86.7372	177	1994-2002, 2004-2008	18
CRANE	Sycamore	SYCA	38.85389	-86.7342	173		4



IDNR	McCormick River	MCRI	39.30306	-86.7339	183		4
IDNR	Martin State Forest 1	MART <sup>b</sup>	38.97139	-86.8556	190		4
IDNR	Martin State Forest 2	MRTS	38.72889	-86.8939	175		4
IDNR	McCormick State Park	MCCR <sup>c</sup>	39.30083	-86.7136	194		4
IDNR	Owen-Putnam State Forest	OWEN	39.32139	-86.8525	237		4
IDNR	Spring Mill State Park	SPMI	38.72778	-86.4297	200		4
BONWR	Area 27 A	A27A	39.00028	-85.3772	280		4
BONWR	Area 03	AR03	39.04639	-85.4389	235	2004-2008	9
BONWR	Area 07	AR07	39.03583	-85.4372	259	1994-2002, 2004-2008	18
BONWR	Area 31	AR31	38.96972	-85.4608	259	1994-2002, 2004-2008	18
BONWR	Area 41	AR41	38.93417	-85.37	273		4
BONWR	Area 58	AR58	38.84806	-85.4553	252		4

a) NSWC Crane Division = CRANE, Indiana Department of Natural Resources State Parks and Forest = IDNR, Big Oaks National Wildlife Refuge = BONWR; b) MART = MRTN in previous reports; c) MCCR = MSTP in previous reports. MAPS station codes changed here for consistency with codes used for intensive monitoring plots.

### Mist-netting effort

All MAPS stations were operated during 2011-2014 according to the standardized protocol established by IBP for use in the MAPS Program (Desante et al. 2015). Mist-netting effort data (i.e., the number and timing of net-hours on each day of operation) were collected in a standardized manner by recording net-opening, net-checking, and net-closing times to the nearest 10 minutes. We aimed to operate nets for six morning hours per day beginning at local sunrise. Inclement weather (especially heavy rain) sometimes resulted in truncated operation on a particular day. Nevertheless, overall effort was fairly consistent among years (Table 2.2).

**Table 2.2** Annual effort (net-hours) completed at the 18 MAPS stations operated in southern Indiana 2011-2014.

Region	Station code	2011	2012	2013	2014
CRANE	FIRS	373	393	403	374
CRANE	SEED	371	377	419	347
CRANE	SULP	370	377	401	413
CRANE	EABO	400	387	389	407
CRANE	AR14	350	390	395	411
CRANE	SYCA	372	408	373	370
IDNR	MART	415	450	458	453
IDNR	MCCR	480	469	438	413
IDNR	MCRI	441	458	442	422
IDNR	MRTS	433	443	462	473
IDNR	OWEN	421	439	455	425
IDNR	SPMI	427	434	432	436
BONWR	AR31	395	445	417	473
BONWR	AR07	464	460	419	469
BONWR	AR03	466	426	396	447
BONWR	AR41	472	469	448	469
BONWR	AR58	427	457	458	435
BONWR	A27A	443	438	387	473

### Breeding status

The breeding (summer residency) status (confirmed breeder, likely breeder, non-breeder) of each species seen, heard, or captured at each MAPS station on each day of operation was recorded

using techniques similar to those employed for breeding bird atlas projects. We classified the landbird species captured in mist nets into six groups based upon their breeding or summer residency status. Each species was classified as one of the following:

- a regular breeder (B) if we had positive or probable evidence of breeding or summer residency within the boundaries of the MAPS station during all 4 years of the study.
- a usual breeder (U) if we had positive or probable evidence of breeding or summer residency within the boundaries of the MAPS station during more than half but not all of the years that the station was operated (here for 3 of the 4 years of the study).
- an occasional breeder (O) if we had positive or probable evidence of breeding or summer residency within the boundaries of the MAPS station during half or fewer of the years that the station was operated (here, 1-2 years).
- A likely breeder (L) if there was at least some indication of breeding in one or more years based on detection(s) during the breeding season, range, and habitat.
- a transient (T) if the species was never a breeder or summer resident at the station, but the station was within the overall breeding range of the species.
- a migrant (M) if the station was not located within the overall breeding range of the species.

Data for a given species from a given station were included in productivity analyses if the station was within the breeding range of the species; that is, data were included from stations where the species was a breeder (B, U, or O), or transient (T), but not where the species was an altitudinal disperser (A) or a migrant (M).

## **Banding**

With few exceptions, all birds captured at MAPS stations were identified to species, age, and sex. If unbanded, the birds were banded with USGS/BRD numbered aluminum bands. Birds were released immediately upon capture and before being banded or processed if situations arose where bird safety was compromised. Such situations could involve exceptionally large numbers of birds being captured at once, or the sudden onset of adverse weather conditions such as high winds or rainfall. The following data were collected from all birds captured, including recaptures:

- capture code (newly banded, recaptured, band changed, unbanded);
- band number
- species
- age and how aged
- sex (if possible) and how sexed (if applicable)
- extent of skull pneumaticization
- breeding condition of adults (i.e., extent of cloacal protuberance or brood patch)
- extent of juvenal plumage in young birds
- extent of body and flight-feather molt
- extent of primary-feather wear
- presence of molt limits and plumage characteristics
- wing chord
- fat class and body mass
- date and time of capture (net-run time)
- station and net site where captured
- any pertinent notes

## **Habitat**

For each of the stations, simple habitat maps were prepared each year that indicated extent and location of major habitats, as well as structures, roads, trails, and streams. Habitat maps subsequent to the initial year were checked and updated whenever necessary. Pattern and extent of cover of each of four major vertical layers of vegetation (upperstory, midstory, understory, and ground cover) in each major habitat type were classified into one of twelve pattern types and eleven cover categories according to guidelines in the MAPS Habitat Structure Assessment Protocol (Nott et al. 2003a).

## **Computer data entry and verification**

The computer entry of all banding data was completed by John W. Shipman of Zoological Data Processing, Socorro, NM. The critical data for each banding record (capture code, band number, species, age, sex, date, capture time, station, and net number) were proofed by hand against the raw data and any computer entry errors were corrected. Computer entry of effort and vegetation data was completed by IBP biologists using custom data entry programs. All banding data were then run through a series of verification programs as follows:

- Clean-up programs to check the validity of all codes entered and the ranges of all numerical data.
- Cross-check programs to compare station, date, and net fields from the banding data with those from the summary of mist netting effort data.
- Cross-check programs to compare species, age, and sex determinations against degree of skull pneumaticization, breeding condition (extent of cloacal protuberance and brood patch), and extent of body and flight-feather molt, primary-feather wear, and juvenal plumage.
- Screening programs which allow identification of unusual or duplicate band numbers or unusual band sizes for each species.
- Verification programs to screen banding and recapture data from all years of operation for inconsistent species, age, or sex determinations for each band number.

Any discrepancies or suspicious data identified by any of these programs were examined manually and corrected if necessary. Wing chord, weight, station of capture, date, and any pertinent notes were used as supplementary information for the correct determination of species, age, and sex in all of these verification processes.

## **Data Analysis**

For our target species, Wood Thrush, we provide estimates of demographic rates, specifically productivity (predicted ratio of young/adult birds) and adult apparent survival probability.

We assessed support for variation in productivity among sites by applying logit-linear models to the MAPS age-specific (hatching-year v. after-hatching-year) capture data. The response variable in models represented the probability of a captured bird being a young (hatching year) bird. We first assessed annual variation in productivity with a generalized linear mixed model that included fixed year effects and zero-mean random station effects and compared results to a model that only included a fixed intercept and random station effects (i.e., “dot” model) using a likelihood ratio test. We then assessed variation among locations (station clusters) by comparing a model with fixed location effects (levels = CRANE, IDNR, BONWR) and random station effects and comparing to a model with only random station effects. Generalized linear mixed models were fit

using the ‘lme4’ package (Bates et al. 2014) in the statistical program R (R Core Team 2015). We assessed variation in productivity among stations with a generalized linear model (‘glm’ function in R) that included fixed station effects and compared to an intercept-only model using a likelihood ratio test. Location- and station-specific reproductive index estimates (*RI*) were derived by exponentiating coefficient estimates from models with intercepts excluded to provide a response metric on the scale of per-capita reproduction (i.e., young/adult; Robinson et al. 2007). Profile confidence intervals (95% CIs) were estimated using the ‘confint’ function in R (R Core Team 2015). To assess the relationship between productivity and the gradient of forest cover represented by the larger intensive demographic monitoring study, we also fit a productivity model that included a covariate calculated for the 12 stations included in the larger project that represented forest cover within 2 km of the station.

To assess apparent adult survival we implemented a Cormack-Jolly-Seber (CJS) model accounting for transients (Hines et al. 2003) to estimate adult apparent survival probabilities at each station with program MARK (White and Burnham 1999) in R (R Core Team 2015) using the R package RMark (Laake 2013). We considered three models to assess spatial variation in survival: 1) no-variation (i.e., intercept-only, or “dot” model); 2) variation among locations (fixed location effect); and 2) variation among stations (fixed station effect. For all models we modeled recapture probability as a logit-linear function of a station-specific covariate representing the mean number of times individuals were captured at the station per season (Saracco et al. 2008). We compared the  $i = 1, \dots, 3$  models using Akaike’s Information Criterion for small samples,  $AIC_c$ , and  $AIC_c$  model weights,  $w_i$  (Burnham and Anderson 2002).

## Results and Discussion

### Breeding Status Lists

We recorded 128 species at the 18 MAPS stations during 2011-2014 (Appendix A). Sixty-two of these species were confirmed as breeding species at one or more stations; nearly all of which were encountered during mist-netting operations (all but Wood Duck and Chimney Swift). The number of breeding species encountered at stations ranged from a low of 54 at A27A (BONWR) to 107 at AR31 (BONWR). The average number of breeding species encountered ranged from a low of 63 at IDNR, to 79 at BONWR, and 84 at CRANE.

### Banding Summary

We captured and banded or recaptured 7,036 individuals of 65 species at the 18 MAPS stations during the course of the study (Table 2.3). We recorded 722 between-year recaptures of these individuals. Wood Thrush was the most commonly captured species, with 1133 year-unique individuals captured, followed by Kentucky Warbler (880 year-unique individuals), and Acadian Flycatcher (692 year-unique individuals). More than 2/3 of the species had fewer than 100 year-unique captures over the four years of the study.

**Table 2.3** Summary of year-unique captures for 65 bird species banded at 18 Monitoring Avian Productivity and Survivorship (MAPS) stations in southern Indiana, 2011-2014.

Common name	Scientific name	2011		2012		2013		2014		Total
		AHY	HY	AHY	HY	AHY	HY	AHY	HY	
American Woodcock	<i>Scolopax minor</i>	0	0	0	0	1	0	0	0	1
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	4	0	0	0	0	0	1	0	5
Red-headed Woodpecker	<i>Melanerpes erythrocephalus</i>	0	0	1	0	0	0	0	0	1

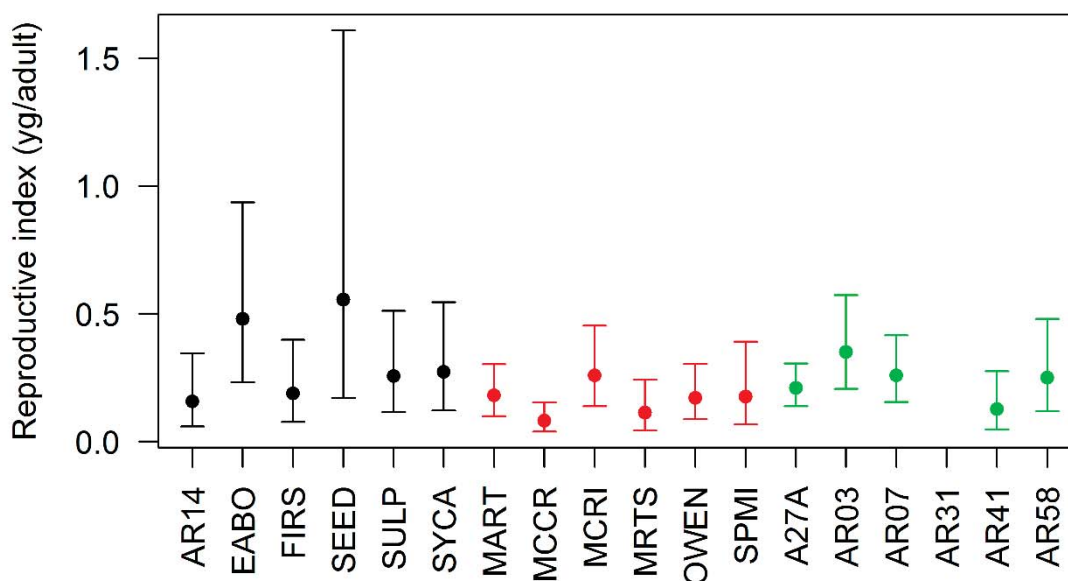
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	5	0	7	2	4	2	3	2	<b>25</b>
Downy Woodpecker	<i>Picoides pubescens</i>	8	15	17	34	20	32	18	28	<b>172</b>
Hairy Woodpecker	<i>Picoides villosus</i>	5	3	8	5	4	8	12	7	<b>52</b>
Yellow-shafted Flicker	<i>Colaptes a. auratus</i>	0	0	0	4	5	0	1	0	<b>10</b>
Eastern Wood-Pewee	<i>Contopus virens</i>	42	1	21	0	30	1	26	1	<b>122</b>
Yellow-bellied Flycatcher	<i>Empidonax flaviventris</i>	0	0	3	0	1	0	0	0	<b>4</b>
Acadian Flycatcher	<i>Empidonax virescens</i>	190	11	154	13	154	15	146	9	<b>692</b>
Traill's Flycatcher	<i>Empidonax alnorum/traillii</i>	11	1	4	0	4	0	0	0	<b>20</b>
Least Flycatcher	<i>Empidonax minimus</i>	0	0	0	0	1	0	0	0	<b>1</b>
Eastern Phoebe	<i>Sayornis phoebe</i>	3	0	4	1	5	0	8	2	<b>23</b>
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	0	0	0	0	0	0	1	0	<b>1</b>
White-eyed Vireo	<i>Vireo griseus</i>	35	11	44	11	34	12	47	15	<b>209</b>
Yellow-throated Vireo	<i>Vireo flavifrons</i>	0	0	4	1	4	0	2	0	<b>11</b>
Red-eyed Vireo	<i>Vireo olivaceus</i>	87	2	73	2	44	1	56	3	<b>268</b>
Blue Jay	<i>Cyanocitta cristata</i>	17	0	10	1	14	2	5	3	<b>52</b>
Carolina Chickadee	<i>Poecile carolinensis</i>	14	13	4	28	20	5	19	19	<b>122</b>
Tufted Titmouse	<i>Baeolophus bicolor</i>	38	29	35	49	40	28	26	24	<b>269</b>
White-breasted Nuthatch	<i>Sitta carolinensis</i>	2	4	6	11	3	6	8	3	<b>43</b>
Carolina Wren	<i>Thryothorus ludovicianus</i>	14	9	29	39	33	31	11	21	<b>187</b>
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	5	0	3	1	7	1	7	2	<b>26</b>
Eastern Bluebird	<i>Sialia sialis</i>	1	0	1	2	1	0	0	0	<b>5</b>
Veery	<i>Catharus fuscescens</i>	0	0	0	0	0	0	1	0	<b>1</b>
Gray-cheeked Thrush	<i>Catharus minimus</i>	7	0	1	0	0	0	13	0	<b>21</b>
Swainson's Thrush	<i>Catharus ustulatus</i>	12	0	9	0	19	0	42	0	<b>82</b>
Wood Thrush	<i>Hylocichla mustelina</i>	215	45	250	43	227	42	247	64	<b>1133</b>
American Robin	<i>Turdus migratorius</i>	23	8	8	4	11	1	8	3	<b>66</b>
Gray Catbird	<i>Dumetella carolinensis</i>	82	12	74	15	63	10	75	14	<b>345</b>
Brown Thrasher	<i>Toxostoma rufum</i>	4	2	2	1	4	1	3	2	<b>19</b>
Cedar Waxwing	<i>Bombycilla cedrorum</i>	0	0	1	0	0	0	1	0	<b>2</b>
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	24	6	26	0	14	3	14	2	<b>89</b>
Tennessee Warbler	<i>Oreothlypis peregrina</i>	0	0	0	0	0	0	1	0	<b>1</b>
Northern Parula	<i>Setophaga americana</i>	1	1	4	1	5	0	1	0	<b>13</b>
Yellow Warbler	<i>Setophaga petechia</i>	0	0	0	0	1	0	0	0	<b>1</b>
Magnolia Warbler	<i>Setophaga magnolia</i>	1	0	1	0	0	0	0	0	<b>2</b>
Yellow-throated Warbler	<i>Setophaga dominica</i>	2	0	0	1	0	0	0	0	<b>3</b>
Prairie Warbler	<i>Setophaga discolor</i>	5	0	13	0	5	2	9	3	<b>37</b>
Bay-breasted Warbler	<i>Setophaga castanea</i>	0	0	0	0	1	0	0	0	<b>1</b>
Cerulean Warbler	<i>Setophaga cerulea</i>	3	2	2	0	2	0	1	1	<b>11</b>
Black-and-white Warbler	<i>Mniotilta varia</i>	4	0	1	1	5	6	2	2	<b>21</b>
American Redstart	<i>Setophaga ruticilla</i>	6	1	6	1	14	3	11	3	<b>45</b>
Prothonotary Warbler	<i>Protonotaria citrea</i>	7	0	7	1	5	0	4	0	<b>24</b>
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	22	9	28	7	14	20	22	18	<b>140</b>
Ovenbird	<i>Seiurus aurocapilla</i>	67	16	65	44	75	29	71	58	<b>425</b>
Louisiana Waterthrush	<i>Parkesia motacilla</i>	24	22	21	27	23	28	32	24	<b>201</b>
Kentucky Warbler	<i>Geothlypis formosa</i>	184	65	168	74	135	56	128	70	<b>880</b>
Connecticut Warbler	<i>Oporornis agilis</i>	0	0	0	0	0	0	1	0	<b>1</b>
Common Yellowthroat	<i>Geothlypis trichas</i>	74	8	90	19	62	7	64	9	<b>333</b>
Hooded Warbler	<i>Setophaga citrina</i>	49	6	65	24	42	15	33	9	<b>243</b>
Canada Warbler	<i>Cardellina canadensis</i>	1	0	1	0	1	0	2	0	<b>5</b>
Yellow-breasted Chat	<i>Icteria virens</i>	33	0	32	6	30	4	34	7	<b>146</b>
Summer Tanager	<i>Piranga rubra</i>	6	1	0	0	4	0	6	1	<b>18</b>
Scarlet Tanager	<i>Piranga olivacea</i>	31	2	30	1	18	3	28	2	<b>115</b>
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	18	8	24	15	25	7	16	2	<b>115</b>
Field Sparrow	<i>Spizella pusilla</i>	12	1	10	1	13	0	5	1	<b>43</b>
Song Sparrow	<i>Melospiza melodia</i>	1	0	5	3	3	1	5	1	<b>19</b>
Northern Cardinal	<i>Cardinalis cardinalis</i>	104	10	67	21	67	24	74	25	<b>392</b>



Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	0	0	3	0	2	0	0	0	<b>5</b>
Indigo Bunting	<i>Passerina cyanea</i>	87	2	88	2	82	6	43	3	<b>313</b>
Red-winged Blackbird	<i>Agelaius phoeniceus</i>	1	0	1	0	0	0	1	0	<b>3</b>
Common Grackle	<i>Quiscalus quiscula</i>	1	1	0	0	0	0	0	0	<b>2</b>
Brown-headed Cowbird	<i>Molothrus ater</i>	9	2	13	3	7	1	10	3	<b>48</b>
American Goldfinch	<i>Spinus tristis</i>	5	0	7	0	13	0	8	0	<b>33</b>

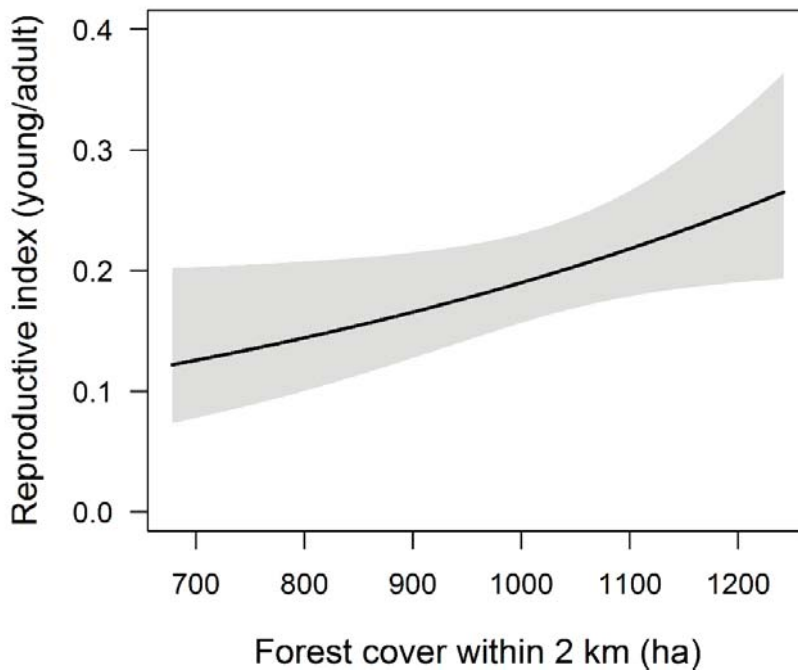
### Wood thrush Productivity

We found no evidence of annual variation in productivity (year effects + random station effect model v. model with only random station effect  $\chi^2 = 3.54$ ; d.f. = 3;  $P = 0.32$ ). We did, however, find strong support for spatial variation in productivity. A model with fixed location (cluster) effects suggested differences in productivity among locations (comparison with random station effect only model:  $\chi^2 = 6.23$ ; d.f. = 2;  $P = 0.04$ ); with productivity lower at IDNR ( $RI = 0.15$ ; 95% CI: 0.11, 0.17) than at BONWR ( $RI = 0.23$ ; 95% CI: 0.17, 0.30) or CRANE ( $RI = 0.27$ ; 95% CI: 0.19, 0.38). Similarly, we found support for variation in productivity among stations (intercept-only model v. model with fixed station effects:  $\chi^2 = 30.37$ ; d.f. = 17;  $P = 0.02$ ). We were able to estimate productivity for 17 stations (too few captures were recorded At station AR31 on BONWR to estimate productivity). Of these, point estimates of productivity (RI) ranged from a low of 0.08 (95% CI: 0.04, 0.15) at MCCR (location: IDNR) to 0.56 (95% CI: 0.17, 1.6) at SEED (location: CRANE; Fig. 2.1).



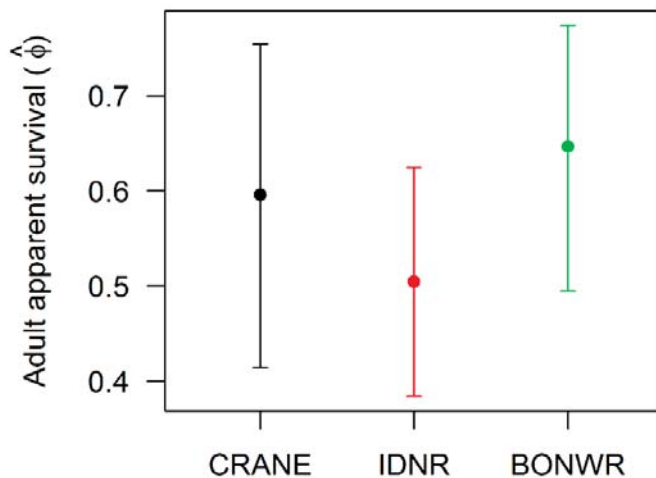
**Figure 2.1** Reproductive index derived as exponentiated station effects from a logit-linear model applied to age-specific capture data from 18 MAPS stations in southern Indiana. Colors denote location groupings. Black=CRANE, Red= IDNR, Green=BONWR.

In considering just stations contained within the intensive monitoring plots, we found little correspondence between the MAPS productivity index values and fecundity estimates from the intensive monitoring plots ( $r = 0.03$ ; df = 10;  $P = 0.92$ ; fecundity estimates presented in Ch. 3). Nevertheless, MAPS productivity was positively related to the amount of forested area within 2-km ( $\hat{\beta} = 0.001$ ;  $SE = 0.001$ ;  $P = 0.032$ ; Fig. 2.2).



**Figure 2.2** Predicted MAPS reproductive index across the range of 2-km forest cover values observed at 12 MAPS stations shared with the intensive demographic monitoring project. Predicted values were derived from a logit-linear model applied to age-specific capture data.

the data ( $\Delta AIC_c = 22.46$ ;  $w_i = 0.44$ ). In contrast to our productivity data, we saw strong correspondence between MAPS survival estimates and those derived from intensive demographic monitoring (Fig. 2.4).



**Figure 2.3** Adult apparent survival rate estimates derived from MAPS data collected at 18 Indiana MAPS stations 2011-2014 from a model including fixed location (cluster) effects. Colors denote location groupings shown for stations in Fig 1.

### Adult apparent survival

The most strongly supported of the three models we considered was the intercept-only model ( $w_i = 0.56$ ). The survival probability estimate from this model was 0.56 (95% CI: 0.45-0.66). The model with location effects was competitive with the intercept-only model, ( $\Delta AIC_c = 0.44$ ;  $w_i = 0.44$ ). Survival probabilities from this model ranged from a low of 0.50 (95%CI: 0.38, 0.62) at IDNR, to 0.60 (95% CI: 0.41, 0.75) at CRANE, to a high of 0.65 (95% CI: 0.50, 0.77) at BONWR (Fig. 2.3).

The model including station effects was not supported by

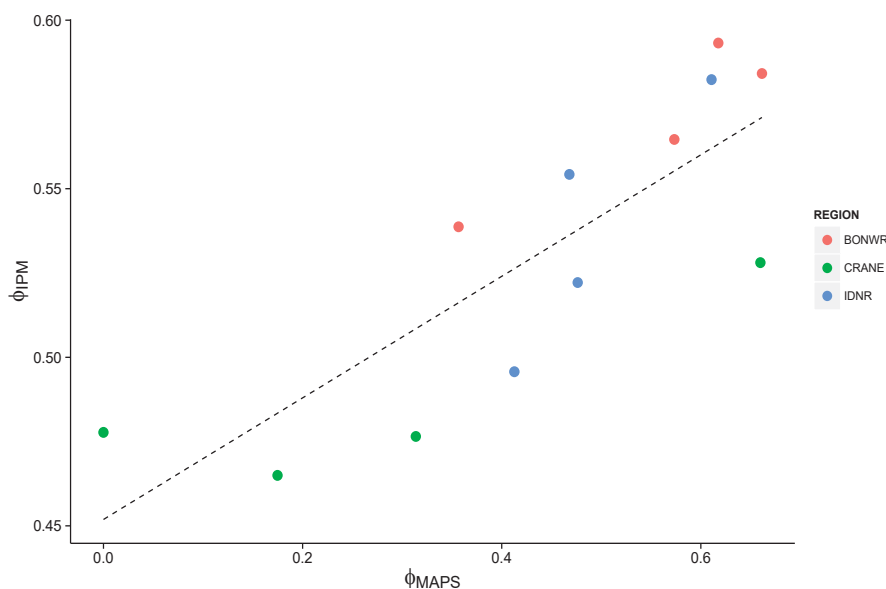
This study provided a rare opportunity for comparing demographic data from MAPS and more intensive demographic monitoring methodologies. While many (albeit not all) studies have found positive correspondence between reproductive index values from constant-effort mist-netting and other fecundity metrics, such as nesting success or numbers of fledglings produced, we found that the station-scale MAPS productivity index for Wood Thrush was not very representative of fecundity values calculated from the intensive monitoring study at 12 stations where both monitoring methodologies were

employed. It is possible that lack of correspondence resulted from differences in age-specific detection probabilities or movements among sites; however, it seems likely that discordance



between estimates largely reflected overall differences in scales of sampling between the two methodologies. Whereas the scale of sampling of the intensive demographic monitoring program was known (40-50 ha), the scale of MAPS sampling was not. Nevertheless, correlation with 2-km radius forest cover suggests that MAPS reproductive index values may reflect habitat quality at a larger landscape scale (> 1000 ha). Correlation with habitat at 2-km radius is consistent with findings of other MAPS habitat analyses (Nott et al. 2003b; 2005). Although this approximate scale may be generally representative of MAPS sampling, we suggest that more study is needed to better understand the scale of MAPS sampling across a variety of species and landscapes.

In addition to providing a point of comparison for the intensive demographic monitoring efforts, the MAPS data collected here represent an important contribution to larger regional and continental demographic monitoring efforts. Indeed, correlation of MAPS productivity indices with population attributes at regional scales suggest that the index is most useful for studies of broader scale demographic patterns (Saracco et al. 2008; Rushing et al. 2016). MAPS sampling completed here provides not only a snapshot of demography for the time window sampled here, but for eight of the stations, also adds to a longer time series of data that can be used to assess trends in demographic rates. We look forward to potential opportunities for continuing this important work in future years.



**Figure 2.4** The positive correlation between apparent survival estimates derived from MAPS monitoring and intensive demographic monitoring. Comparison of apparent survival estimates was only possible for the 12 intensive demographic sites that were paired with MAPS station in the study design.

## Conclusions and Implications for Future Research

The results of the MAPS monitoring provide important insight into Wood thrush population dynamics at both the local and regional scale. MAPS data as presented here were able to provide vital demographic information about 65 species of forest birds many of which have shown sharp declines over the last decade. Although vital rates (productivity and survival) are only highlighted for the focal species of the grant, Wood thrush, future work will examine comparable analyses for a host of species to examine similarities/ differences in demographic performance on DoD installations. Our results show that apparent survival rates from MAPS and intensive demographic approaches are highly correlated. Overall, MAPS estimates tend to be biased low

because this methodological approach does not invest time and energy into unique color-marking and resighting effort. This reduction in effort makes MAPS more cost effective if the primary management goal is to only estimate apparent survival. In contrast, we found little correspondence between the MAPS reproductive index and measures of fecundity derived from intensive demographic monitoring. These results underscore potential issues of scale and suggest that the MAPS approach may not be capturing local productivity. Regardless, MAPS data does appear to be able to tell us about regional trends and can be used to understand how regional land-use impacts avian species of concern. Future analytical research will need to be focused on how MAPS data can inform the scale of avian population dynamics. Moreover, insight from the dynamic occupancy modeling presented in Chapter 1 strongly suggest that the influence of temporary emigration may also lead to bias in the estimation of demographic vital rates.

### Literature Cited

- Albert, S. K., D. F. DeSante, D. R. Kaschube, and J. F. Saracco. (2016) MAPS (Monitoring Avian Productivity and Survivorship) data provide inferences on demographic drivers of population trends for 158 species of North American landbirds. *North American Bird Bander*, **41**, 133–140.
- Bart, J., C. Kepler, P. Sykes, and C. Bocetti. (1999) Evaluation of mist-net sampling as an index to productivity in Kirtland’s warblers. *Auk*, **116**, 1147–1151.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. (2014) lme4: Linear mixed-effects models using Eigen and S4. *R package version 1.0-6*.
- Burnham, K., and D. Anderson. (2002) Model selection and multi-model inference: a practical information theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.
- Desante, D. F., K. M. Burton, P. Velez, D. Froehlich, and D. R. Kaschube. (2015) MAPS Manual: 2015 Protocol. The Institute for Bird Populations, Point Reyes Station, CA USA.
- DeSante, D. F., and D. R. Kaschube. (2009) The Monitoring Avian Productivity and Survivorship (MAPS) Program 2004, 2005, and 2006 Report. *Bird Populations*, **9**, 86–169.
- DeSante, D. F., D. R. Kaschube, and J. F. Saracco. (2015) Vital Rates of North American Landbirds. [www.VitalRatesOfNorthAmericanLandbirds.org](http://www.VitalRatesOfNorthAmericanLandbirds.org).
- George, T. L., R. J. Harrigan, J. A. LaManna, D. F. DeSante, J. F. Saracco, and T. B. Smith. (2015) Persistent impacts of West Nile virus on North American bird populations. *PNAS*, 1507, 747112.
- Hines, J. E., W. L. Kendall, and J. D. Nichols. (2003) On the use of the robust design with transient capture-recapture models. *Auk*, **120**, 1151.
- Laake, J. L. (2013) RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01. Seattle, WA.
- LaManna, J. A., T. L. George, J. F. Saracco, M. P. Nott, and D. F. DeSante. (2012) El Niño–Southern Oscillation influences annual survival of a migratory songbird at a regional scale. *Auk*, **129**, 734–743.
- Nott, M., D. DeSante, and N. Michel. (2003a) Monitoring avian productivity and survivorship (MAPS) habitat structure assessment (HSA) protocol. Point Reyes Station, CA USA.
- Nott, M. P., D. F. DeSante, and N. Michel. (2003b) Management strategies for reversing declines in landbirds of conservation concern on military installations: a landscape scale analysis of MAPS data. Point Reyes Station, CA USA.
- Nott, M. P., D. F. DeSante, P. Pyle, and N. Michel. (2005) Pacific Northwest forest bird population declines: formulating population management guidelines from a landscape scale ecological analyses of MAPS data from avian communities on seven national forests of the Pacific

- Northwest. Point Reyes Station, CA USA.
- Nott, M. P., D. F. Desante, R. B. Siegel, and P. Pyle. (2002) Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America. *Global Ecology and Biogeography*, **11**, 333–342.
- R Core Team. (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
- Ralph, C. J., and E. H. Dunn. (2004) Use of mist nets as a tool for bird population monitoring. *Studies in Avian Biology*, **29**, 1–6.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. (1993) Handbook of Field Methods for Monitoring Landbirds. USDA Forest Service General Technical Report PSW-144, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.
- Robinson, R. A., S. N. Freeman, D. E. Balmer, and M. J. Grantham. (2007) Cetti's Warbler *Cettia cetti*: analysis of an expanding population: Capsule Productivity in the UK Cetti's Warbler population is constant, but overwinter survival has become increasingly dependent on winter temperatures. *Bird Study*, **54**, 230–235.
- Rushing, C. S., T. B. Ryder, A. L. Scarpignato, J. F. Saracco, and P. P. Marra. (2016) Using demographic attributes from long-term monitoring data to delineate natural population structure. *Journal of Applied Ecology*, **53**, 491–500.
- Ryu, H. Y., K. T. Shoemaker, É. Kneip, A. M. Pidgeon, P. J. Heglund, B. L. Bateman, W. E. Thogmartin, and H. R. Akçakaya. (2016) Developing population models with data from marked individuals. *Biological Conservation*, **197**, 190–199.
- Saracco, J. F., D. F. Desante, and D. R. Kaschube. (2008) Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends. *Journal of Wildlife Management*, **72**, 1665–1673.
- Saracco, J. F., J. A. Royle, D. F. DeSante, and B. Gardner. (2010) Modeling spatial variation in avian survival and residency probabilities. *Ecology*, **91**, 1885–1891.
- Saracco, J. F., J. A. Royle, D. F. DeSante, and B. Gardner. (2012) Spatial modeling of survival and residency and application to the Monitoring Avian Productivity and Survivorship program. *Journal of Ornithology*, **152**, 469–476.
- White, G., and K. Burnham. (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46**, 120–138.

## **Chapter 3- Demography across the annual cycle: spatial and temporal variation in vital rates drives population dynamics in a migratory bird**

### **Abstract**

Untangling the spatial and temporal processes that influence population dynamics remains one of the great ecological challenges because demographic data must be collected and integrated across multiple scales. This problem is especially acute for migratory species due to the scale of their annual movements and the fact that population dynamics are jointly shaped by variation in vital rates across heterogeneous habitats and throughout the annual cycle. Here, we use intensive demographic data across 12 breeding sites in southern Indiana and 4 non-breeding sites in Belize to parametrize a full-annual-cycle integrated population model to estimate stage-specific demographic rates, including survival during both spring and fall migration, and their contribution to population growth. We demonstrate the utility of this approach using demographic data from a declining migratory songbird, the Wood Thrush (*Hylocichla mustelina*), collected across a breeding habitat quality gradient and on its wintering grounds. We found that variance in population growth was most strongly determined by variation in spring migration survival, but also that the relative contribution of vital rates to population growth was habitat-specific. Population growth in high-quality habitat was most sensitive to variation in fecundity and migration survival, whereas in low-quality sites, population growth was most sensitive to adult breeding-season survival. These results elucidate how full-annual-cycle vital rates, particularly migration survival, interact with spatial variation in habitat quality to influence population dynamics in a migratory species.

### **Objective**

Here, we use intensive demographic monitoring to estimate multiple vital rates and understand their contribution to population dynamics across a habitat quality gradient. Our intensive demographic monitoring effort took a full-annual cycle approach monitoring vital rates for Wood thrush during both the breeding and non-breeding season. We identified linked populations (Indiana and Belize) using data from light-level geolocators. During the breeding season characterized the following vital rates: apparent adult survival, fecundity, rebreeding probability and post-fledging survival. On the non-breeding grounds, we collected apparent adult survival. The objectives with this data were to: 1) build a full-annual cycle integrated population model, 2) examine the relative contributions of different vital rates to variation in population growth and identify sources and sinks and 3) understand how variation in habitat quality (local habitat structure) influences population growth. Overall, these analyses enabled us to characterize which vital rates and habitat characteristics drive population change.

### **Background**

Determining how and why populations change in abundance (i.e., population dynamics) has been a central focus of ecology since its inception. For most vertebrate populations, however, we still lack an understanding of how complex spatial and temporal processes interact to influence population growth and subsequent persistence (Oro 2013). Numerous theoretical models have been developed to examine how vital rates (i.e., survival, reproductive output, emigration, and immigration) contribute to temporal (Sutherland 1996; Runge & Marra 2005) and spatial (Pulliam 1988; Hanski 1999) variation in population growth, but empirical validations of these models

rarely account for both spatial heterogeneity in habitat quality or temporal stochasticity in environmental conditions (Pearson & Fraterrigo 2011). Given the scale and severity of environmental change in terrestrial ecosystems, developing a framework that can quantify the drivers of population dynamics across space and time is critical to advancing basic ecological theory and conservation.

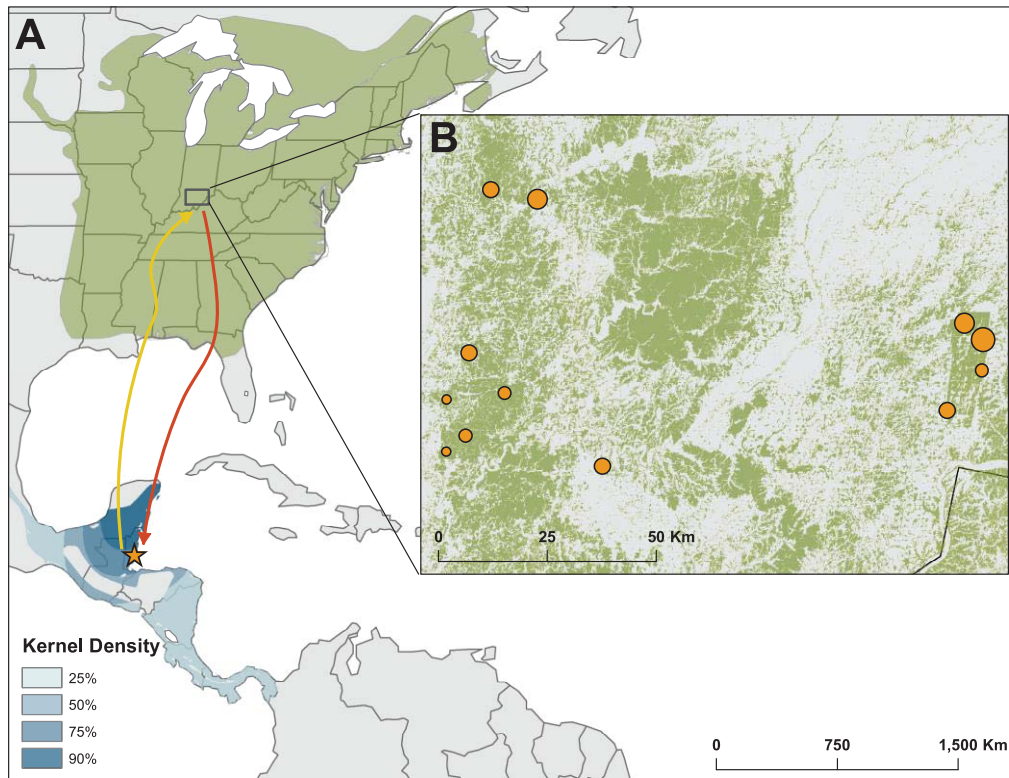
The challenges of quantifying vital rates and their contribution to population dynamics are magnified for migratory animals because large-scale seasonal movements can induce complex spatiotemporal interactions that shape population processes (Nichols 1996). Understanding how demographic processes affect population dynamics in these species is difficult because limitation can occur at any stage of the annual cycle, including breeding, wintering, and autumn and spring migration (Sherry & Holmes 1995; Sutherland 1996). To further complicate matters, stage-specific demographic and environmental processes often interact such that no single period can be understood outside the context of the entire cycle (Marra et al. 2015). Although some progress has been made in quantifying stage-specific survival for game species (Ward et al. 1997) and large-bodied species capable of carrying satellite transmitters (Klaassen et al. 2014; Lok et al. 2015), estimates of survival during spring and fall migration are unavailable for the vast majority of migratory species. In addition, understanding how stage-specific vital rates influence population dynamics requires models that can integrate demographic data from across the annual cycle. Full-annual-cycle models have been developed for several well-studied waterfowl species (Mattsson et al. 2012; Robinson et al. 2016b), but application of these frameworks to other migratory species have been hindered by the inability to track individuals throughout the annual cycle, missing information on the linkages between breeding and wintering populations (i.e., migratory connectivity), and the lack of large-scale demographic monitoring data for linked populations.

The relative contribution of vital rates to population dynamics is also unlikely to be uniform across space because migratory species typically inhabit heterogeneous habitats. A number of studies have documented habitat-specific vital rates (Holmes et al. 1996; Murphy 2001; Pereira & Novaro 2014) and population growth rates (Kreuzer & Huntly 2003; Getz et al. 2005), yet we know little about the differential contribution of vital rates to population growth across heterogeneous habitats. Many processes, including density-dependent dispersal (Gundersen et al. 2001), covariance among vital rates (Sæther & Bakke 2000; Sim et al. 2011), and seasonal interactions (Runge & Marra 2005) could influence the relative importance of each vital rate to population growth among habitats that differ in quality. The contribution of vital rates may also be scale-dependent such that certain rates (e.g., fecundity and immigration) may be more important at local scales and others at regional scales (Diez & Giladi 2011). Ultimately, understanding how spatial variation influences the relative contribution of vital rates to population growth, and how this spatial variation interacts with temporal processes are essential elements of vertebrate population ecology and conservation science.

The development of integrated population models (IPMs) provides a powerful framework for combining multiple data sources (e.g., counts, mark-recapture, reproductive monitoring) to improve estimation of vital rates and their contribution to population growth. Recent applications of these models have provided insights into the demographic processes that drive population dynamics of several species (Schaub et al. 2007; Rhodes et al. 2011; Chandler & Clark 2014). To date, however, IPMs have focused solely on estimation of vital rates and their influence on population dynamics during a single stage of the annual cycle (e.g., breeding: Robinson et al. 2014; wintering: Weegman et al. 2016). Ultimately, advancing our understanding of how spatial and temporal factors drive population dynamics for migratory animals necessitates a model framework



that can characterize demographic processes across the entire annual cycle (Hostetler et al. 2015). Here, we present a full-annual-cycle IPM parameterized using habitat-specific demographic data collected from a migratory songbird, the Wood Thrush (*Hylocichla mustelina*). By integrating data during the breeding and wintering periods, we were able to estimate stage-specific vital rates, including survival during spring and fall migration, and assess the contribution of each rate to spatial and temporal variation in population growth rate ( $\lambda$ ). Results from this analysis estimate the contribution of stage- and habitat-specific vital rates to population dynamics of a migratory bird, information needed to advance conservation planning.



**Figure 3.1** Map of study sites and demographically linked populations of Wood Thrush used to parameterize the full-annual-cycle IPM. A) Wood Thrush breeding range is shown in green and the winter range in blue. Population linkages (migratory connectivity) were estimated from light-level geolocators (see Stanley et al. 2015) and the kernel density plot shows the estimated probability distribution of wintering Wood Thrush tracked from our breeding population. The approximate autumn (red) and spring (yellow) migration route of one individual is shown. The orange star represents the non-breeding study location at Belize Foundation for Research and Environmental Education. B) Regional forest cover and the distribution of the 12 breeding study plots distributed across southern Indiana, USA. Orange points denote the geographic location of study plots and point size indicates count of trees > 30 cm DBH, a proxy for Wood Thrush habitat quality.

## Methods

### Field Methods

Here, we present a truncated version of the methods, but a full version of both field and analytical approach is presented in Appendix A. Breeding fieldwork was conducted from 2011 to 2014 at 12 study sites across southern Indiana, USA (Fig. 3.1; Appendix Table A1). Starting on the third week of April each year, we systematically surveyed each plot to locate all adult Wood Thrush pairs and nesting attempts. Territorial adults ( $n = 1807$ ) were captured in mist nets, banded with a USGS aluminum band and a unique combination of colors bands, aged (second-year or after



second-year), sexed using molt and plumage criteria, measured (unflattened wing chord and tarsus length), and weighed. After initial marking, we revisited each territory every 3-5 days to conduct extensive resighting efforts for each color-banded individual. All nests ( $n = 946$ ) were monitored approximately every three days to record hatching success (fledge or fail) and the number of offspring. Detailed 5m radius vegetation plots were conducted at all nest following the sampling protocol outlined for point-counts in Chapter 1. Prior to fledging (~day 8), all nestlings ( $n = 1346$ ) were banded with a plot/year specific color combination. At the time of banding, 210 late stage nestlings were fitted with radio-transmitters to estimate post-fledging survival. Each individual was located every 2-3 days until either known death or day 30 post-fledging.

Winter mark-recapture data was collected in the southern region of the Maya Mountains, Toledo District, Belize. We selected Belize as it should be representative of the winter conditions experienced by Wood Thrush breeding in southern Indiana (Stanley et al. 2015; Fig. 3.1). Two banding sites were located on the Belize Foundation for Research and Environmental Education's field station and two were in the Bladen Nature Reserve. At each site, banding was conducted in five monthly pulses (November - March) from 2003 to 2013. During each pulse, banding was conducted over two consecutive days using 16 mist nets. Upon initial capture, each individual ( $n = 1388$ ) was fitted with a uniquely numbered USGS aluminum band, aged, weighed, and measured (as for breeding birds, see above). Upon recapture, each individual's band number was recorded and the same morphological measures were taken. See supplementary information (SI1) for details regarding breeding and winter data collection.

### **Integrated population model**

Using the breeding and wintering demographic data, we estimated vital rates and population growth using a female-only, two age-class integrated population model (IPM). Complete model parameterization is provided in Appendix A (see Table A2). The model consisted of six conditionally related sub-models that link the demographic data to the state variables of interest:

*State-space model to estimate population size:* For each study plot, the total population in each year ( $N_{p,t}$ ) consisted of three classes of individuals: local recruits, surviving adults, and immigrants (Kéry & Schaub 2012). The numbers of local recruits and surviving adults changed annually as a function of fecundity, survival, and population size in previous year. The number of immigrants was treated as a latent variable which was informed by both demographic rate estimates and the count data (Schaub & Abadi 2010). The total abundance on each plot in each year was then linked to the observed population size (total number of active nests on each plot) using a Poisson observation model (Kéry & Schaub 2012).

*Poisson GLM to estimate fecundity:* For each plot, annual per capita fecundity ( $f_{p,t}$ ) was estimated using as a Poisson generalized linear model that linked the total number of offspring in each year to the total number of females in the population (Kéry & Schaub 2012). We used a linear model with a random plot  $\times$  year interaction to estimate spatial and temporal variation in fecundity. The estimated fecundity from nest-monitoring data potentially underestimates true fecundity due to movement between rebreeding or double brooding attempts. To account for this potential bias, we measured the total reproductive success of 77 female Wood Thrush that were radio-tracked on our study plots as part of a separate study. We then used the ratio of the total reproductive success for known-fate females to the nest-monitoring based estimates from the same years and plots to obtain estimates of true fecundity.

*Known-fate model to estimate post-fledging survival:* We estimated daily post-fledging survival probabilities by converting the fledgling radio-tracking data into daily capture histories (1 = known alive, 0 = known dead) from day 1 post-fledging until either the individual's fate became unknown (i.e., censored) or until day 30 post-fledging. For each year  $t$  and plot  $p$ , we used a linear model with random year and plot  $\times$  day effects to estimate spatial and temporal variation in daily survival probability. Annual plot-specific post-fledging survival probability (i.e., survival to 30 days post-fledging) was then estimated as the product of the 29 daily estimates.

*Cormack-Jolly-Seber model to estimate juvenile survival:* Using the breeding mark-resight data from individuals originally captured as free-flying hatch year birds at the end of the breeding season, we developed a Cormack-Jolly-Seber (CJS) model to estimate the apparent juvenile survival (i.e., September - April) while accounting for imperfect detection (Kéry & Schaub 2012). Annual and plot-specific variation in juvenile survival was modeled as linear function of random year and plot effects.

*CJS models with transients to estimate adult survival:* We used the breeding mark-resight and winter mark-recapture data to estimate adult survival both within and between stationary periods. Because Wood Thrush are known to move extensively within both the breeding and wintering periods, we used a modification of the basic CJS model to obtain unbiased estimates of apparent survival while accounting for transients (Pradel et al. 1997). Initial analysis of these data indicated no difference in over-winter survival for juveniles and adults so we pooled these individuals and estimated a single over-winter survival probability. The breeding capture data consisted of 4 monthly capture occasions (May - August) in each year (2011-2014) and three between-breeding occasions. The winter data consisted of 5 monthly occasions (November - March) in each year (2011-2013) and two between-winter occasions. For the breeding model, we modeled monthly survival as a linear function of random annual and month  $\times$  plot effects. A similar model was used to estimate monthly winter survival probabilities, but without plot-level variation. Because the winter capture data ended in 2013, we modeled monthly winter survival in 2014 as the mean of the long-term estimates. For each stationary period (breeding or winter), annual stage-specific survival was estimated as the product of the monthly survival estimates.

The joint likelihood of the integrated model was estimated using JAGS (Plummer 2003) called from R (R Development Core Team 2015) using the package *jagsUI* (Kellner 2016). See supplementary information (SI1) for details regarding model structure, prior distributions, and MCMC estimation.

For each plot, annual and overall population growth rates ( $\lambda_p$ ) were derived directly from the vital rate estimates (Pulliam 1996). In some cases, populations that cannot support themselves through local recruitment processes may experience positive populations growth ( $\lambda_p > 1$ ) due to high immigration rates. Therefore, we also calculated annual and mean self-recruitment rates (Runge et al. 2006), denoted  $R_p$ , by removing immigration from estimates of  $\lambda_p$ . Thus,  $R_p > 1$  indicates plots that were able to maintain or increase abundance through local recruitment processes only and we interpreted self-recruitment rate as a demographic measure of habitat quality. Initial inspection of the  $R_p$  values indicated that self-recruitment rate was highly correlated with the number of large trees (DBH > 30 cm) on each plot ( $\rho = 0.80$ ,  $p < 0.001$ ), which itself is highly predictive of Wood Thrush occupancy in southern Indiana (J.V. Valente & T.B. Ryder *unpub. data*), suggesting that the presence of large trees is the primary habitat feature that determines habitat quality for Wood Thrush in this region.

### Estimating migration and annual survival

The CJS models used to estimate stationary period survival also provide estimates of apparent survival from the end of the stationary period to the beginning of the next (i.e., September to April for breeding model; April - October for winter model). These between-season survival estimates contain information about the latent migration period survival and when combined, the stationary period and between-season survival estimates provide complementary information that can be used to estimate spring and autumn migration survival. The plot-specific estimates of adult survival between breeding seasons (denoted  $\phi_{BBp,t}^{Ad}$ ) from the CJS model are equivalent to:

$$\phi_{BBp,t}^{Ad} = \phi_{Autumn_{p,t-1}}^{Ad} \phi_{Winter_{t-1}} \phi_{Spring_{p,t}}^{Ad}$$

where  $\phi_{Winter_{t-1}}$  is the over-winter survival estimate from the winter CJS model, and  $\phi_{Autumn_{p,t-1}}^{Ad}$  and  $\phi_{Spring_{p,t}}^{Ad}$  are the estimated survival during autumn and spring migration, respectively.

Likewise, adult survival between winters ( $\phi_{BW_t}^{Ad}$ ) is equivalent to:

$$\phi_{BW_t}^{Ad} = \hat{\phi}_{Spring_{p,t}}^{Ad} \hat{\phi}_{Summer_t} \hat{\phi}_{Autumn_{p,t}}^{Ad}$$

where  $\hat{\phi}$  is the mean stage-specific survival estimate across all plots. For juveniles, survival between breeding seasons is estimated in the same way as for adults. However, once wintering juveniles reach the breeding grounds, they become adults. Therefore, survival between winters for juveniles is:

$$\phi_{BW_t}^J = \hat{\phi}_{Spring_{p,t}}^J \hat{\phi}_{Summer_t} \hat{\phi}_{Autumn_{p,t}}^{Ad}$$

For both juveniles and adults, the presence of each latent annual migration survival estimate in multiple equations allows these rates to be estimated within the integrated framework (Appendix Fig. A1).

### Vital rate contributions to population growth

We used life table response experiments (LTRE) to measure the contribution of each vital rate to annual population change while accounting for temporal variation in each rate and the covariance among rates (Caswell 2001; Robinson et al. 2014). We first estimated the posterior mean of the pair-wise covariance between vital rates and multiplied this mean matrix by the sensitivity matrices from each of the 30,000 posterior samples. The contribution of each rate was then estimated by summing the variances and covariances for each parameter and scaling the contributions to sum to 1 (Robinson et al. 2014). For each vital rate, we used the 95% highest posterior density interval (HPDI) to quantify uncertainty in contributions. In addition to quantifying contributions of the full-annual-cycle vital rates, we also estimated contributions from the overall rates typically used in most matrix population models (i.e., fecundity, juvenile apparent survival, annual adult survival, and immigration). To understand how contributions vary across spatial scales, we estimated contributions of each vital rate at both the regional scale (using the mean rates across all plots) and at the local (i.e., plot) scale.

## Results and Discussion

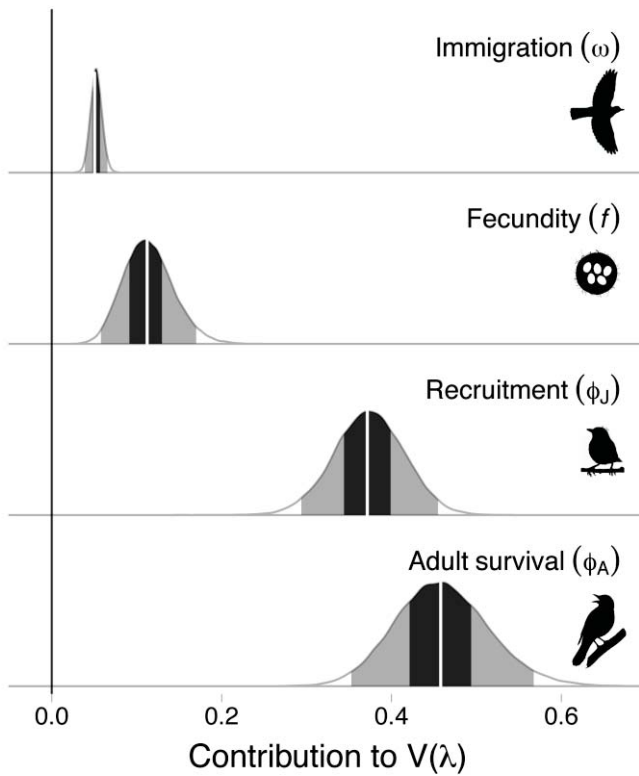
Fecundity estimates were based on 1346 fledglings from 946 nests and radio tracking of 77 breeding females. Juvenile annual survival was estimated from 209 individuals originally banded as nestlings, of which 21 (10.05%) recruited into our breeding populations and were resighted in subsequent years. Estimates of adult survival within and between breeding seasons were based on 1807 individuals, of which 780 (43.17%) were recaptured on  $\geq 1$  occasion. Post-

fledging survival estimates were based on 210 known-fate individuals tracked using radio telemetry. Non-breeding survival within and between winter seasons was estimated from 1388 individuals, of which 399 (28.75%) were recaptured on  $\geq 1$  occasion.

When pooled across the 12 study plots, this population experienced positive, but uncertain growth across the four years of our study ( $\lambda = 1.08$ , 95% HPDI = 0.78:1.39). Population growth, however, was partially driven by a high immigration rate ( $\omega = 0.34$ , 0.21:0.46) and as a result, the self-recruitment rate (i.e., the expected rate of population growth in the absence of immigration) was  $< 1$  ( $R = 0.9$ , 0.48:1.3). Thus, in the absence of continued immigration from outside sources, this population would likely have declined over the course of our study. Despite the importance of immigration to maintaining the regional population, annual variation in population growth was most strongly driven by adult survival and juvenile recruitment (Table 3.1; Fig. 3.2).

**Table 3.1** Vital rate estimates and contributions to variation in population growth for Wood Thrush breeding in southern Indiana (2011-2014). Estimates of the vital rates and their contributions are the posterior means and 95% highest density posterior interval (HPDI) pooled across all years and all demographic plots. Seasonal survival estimates have been scaled to their equivalent monthly survival rates to aid comparison. The annual range provides the posterior means for minimum and maximum annual estimates across the four years of our study. Coefficient of variation is measured as the standard deviation of the annual vital rate estimates divided by the mean. Note that winter survival was not estimated as a function of age and therefore only one estimate is provided. The contribution of juvenile winter survival was negligible (posterior mean = 0.002, 95% HPDI = 0:0.0005) and therefore only the contribution of adult winter survival is shown.

Vital Rate	Mean (95% HDPI)	Annual range	Coef. Variation	Contribution (95% HPDI)
<i>Overall</i>				
Fecundity ( $f$ )	1.84 (1.25:2.46)	1.43:2.25	0.21	0.11 (0.06:0.17)
Immigration ( $\omega$ )	0.34 (0.21:0.46)	0.33:0.36	0.04	0.06 (0.04:0.09)
Recruitment ( $\phi$ )	0.24 (0.17:0.32)	0.16:0.33	0.35	0.37 (0.29:0.45)
Adult annual survival ( $\phi^{Ad}$ )	0.58 (0.46:0.69)	0.56:0.61	0.05	0.46 (0.35:0.57)
<i>Seasonal</i>				
Adult summer survival ( $\phi_{Summer}$ )	0.96 (0.91:0.99)	0.95:0.96	0.02	0.14 (0.07:0.22)
Winter survival ( $\phi_{Winter}$ )	0.98 (0.95:1)	0.98:0.98	0.01	0.06 (0.03:0.1)
Adult autumn survival ( $\phi_{Autumn}^{Ad}$ )	0.92 (0.84:1)	0.92:0.93	0.01	0.11 (0.05:0.17)
Adult spring survival ( $\phi_{Spring}^{Ad}$ )	0.89 (0.71:1)	0.85:0.92	0.04	0.14 (0.07:0.23)
Post-fledging survival ( $\phi_{PF}$ )	0.65 (0.44:0.86)	0.54:0.78	0.16	0.12 (0.07:0.19)
Juvenile autumn survival ( $\phi_{Autumn}^J$ )	0.92 (0.77:1)	0.91:0.92	0.01	0.01 (0:0.01)
Juvenile spring survival ( $\phi_{Spring}^J$ )	0.48 (0.16:0.83)	0.38:0.58	0.23	0.24 (0.1:0.37)



**Figure 3.2** Posterior distributions of the proportional contribution of overall demographic rates to regional annual population growth for Wood thrush breeding in southern Indiana, USA. For each demographic rate, the white line indicates the posterior mean and the dark grey and light grey areas indicate the 50% and 95% highest posterior density intervals, respectively. The demographic rates are ranked on the y-axis by their posterior means, from smallest to largest contribution.

### Stage-specific vital rates and their contribution to population growth

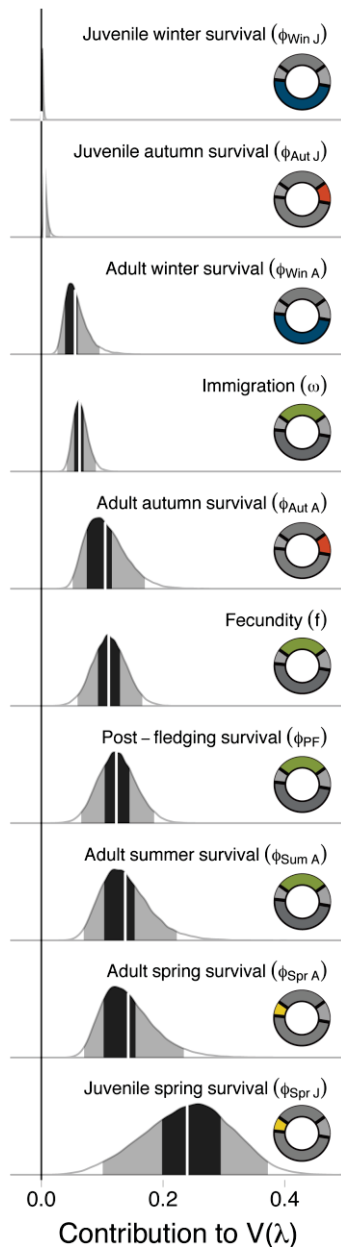
Combining demographic data from linked populations within a full-annual-cycle IPM allowed us to parse adult and juvenile survival into their stage-specific components. Mean apparent adult survival was highest during winter ( $\phi_{Winter}^A = 0.9$ , 95% HPDI = 0.78:1), followed by spring migration ( $\phi_{Spring}^A = 0.89$ , 0.71:1), autumn migration ( $\phi_{Autumn}^A = 0.85$ , 0.7:1), and summer ( $\phi_{Summer}^A = 0.84$ , 0.69:0.97). Thus, spring and autumn migration account for 21% and 29% of adult apparent mortality even though these stage composed only 8.33% and 16.67% of the annual cycle. However, comparison of overall survival during each stage does not indicate how risk (i.e., survival per unit time) varies across the annual cycle because the four seasons of the annual cycle differ in length (winter = 5 months, spring = 1 month, summer = 4 months, autumn = 2 months). When scaled to the

equivalent monthly survival rates, survival was lowest during spring migration (Table 3.1), indicating this is the riskiest stage of the annual cycle for adult Wood Thrush.

Apparent survival of juveniles was highest during winter ( $\phi_{Winter}^J = 0.9$ , 0.78:1), followed by autumn migration ( $\phi_{Autumn}^J = 0.84$ , 0.59:1), post-fledging ( $\phi_{PF} = 0.65$ , 0.44:0.86), and spring migration ( $\phi_{Spring}^J = 0.48$ , 0.16:0.83). Monthly survival probability for juveniles showed a similar pattern (Table 3.1). As a result, spring migration and the post-fledging period accounted for 46% and 31% of juvenile apparent mortality, respectively, whereas autumn migration accounted for only 14%.

Season- and stage-specific vital rates had different, relative effects on  $\lambda$ . Consistent with the high apparent mortality during spring migration, survival of juveniles and adults during this stage had the largest contributions to variation in  $\lambda$  (Table 3.1; Fig. 3.3). Adult summer survival, post-fledging survival, fecundity, and adult fall migration survival also had mean contributions greater than 10%. The remaining vital rates, winter survival and juvenile fall migration survival,





**Figure 3.3** Posterior distributions of the proportional contribution of seasonal demographic rates to regional annual population growth for Wood thrush breeding in southern Indiana, USA. For each demographic rate, the white line indicates the posterior mean and the dark grey and light grey areas indicate the 50% and 95% highest posterior density intervals, respectively. The demographic rates are ranked ordered on the y-axis by their posterior mean contribution to population growth. Colored circles indicate the stage of the annual cycle during which each demographic rate was measured (green = breeding, red = autumn migration, blue = winter, yellow = spring migration).

had smaller effects (<6%) indicating that survival during these stages has little direct impact on population dynamics for this population.

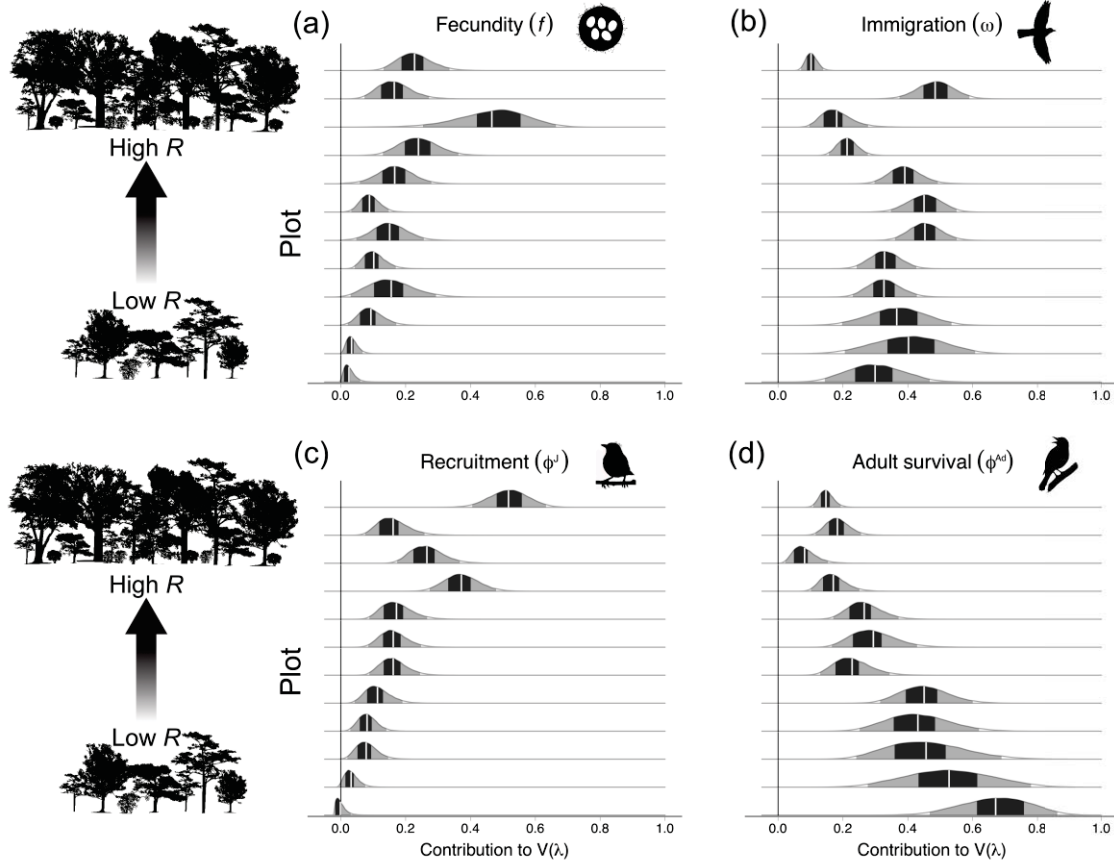
### Habitat-specific vital rates and their contribution to population growth

Mean vital rates, their relative contributions to  $\lambda$ , and  $\lambda$  itself varied among our 12 study plots (Fig. 3.4; Appendix Tables S3-S14). Nine (75%) grew over the four years of the study ( $\lambda > 1$ ), but only four (33.33%) had self-recruitment rates  $> 1$  (Tables S3-S14). Self-recruitment rate was negatively correlated with immigration rate ( $\rho = -0.86$ ,  $P < 0.001$ ) and positively correlated with adult summer survival ( $\rho = 0.95$ ,  $P < 0.001$ ) and fecundity ( $\rho = 0.74$ ,  $P = 0.01$ ). Thus, high-quality plots tended to have higher productivity, higher adult breeding survival and/or site fidelity, and lower immigration. The contributions of recruitment and fecundity to  $\lambda$  tended to be larger in plots with high self-recruitment rates (Fig. 3.4; recruitment:  $\rho = 0.87$ ,  $P < 0.001$ ; fecundity:  $\rho = 0.69$ ,  $P = 0.01$ ), while the contribution of adult survival tended to be larger in plots with low self-recruitment rates ( $\rho = -0.91$ ,  $P < 0.001$ ). The contribution of immigration to  $\lambda$  did not vary as a function of self-recruitment rate ( $\rho = -0.43$ ,  $P = 0.17$ ). In general, these results were driven by a larger contribution of juvenile spring migration survival in higher-quality plots, and a larger contribution of adult summer survival in low-quality plots.

Understanding the demographic processes that shape population dynamics is critical to advancing ecological theory and to designing effective management strategies for species of conservation concern. Like many long-distance migratory species, the Wood Thrush has experienced population declines over the past 50 years, but the demographic causes of these declines remain poorly understood (Rushing et al. 2016a; Taylor & Stutchbury 2016). Consistent with life history theory and empirical studies of similar iteroparous passerines with relatively long lifespans (Norman & Peach 2013; Robinson et al. 2014), our analysis indicates that population dynamics of Wood Thrush breeding in southern Indiana are most strongly driven by variation in adult survival and juvenile recruitment. However, for Wood Thrush and other migratory species, vital rates can vary substantially across the stages of the annual cycle (Silllett & Holmes 2002; Klaassen et al. 2014) and across habitats. We used a novel



full-annual-cycle IPM to show that spring migration is a key determinant of population growth, but also that the relative contribution of vital rates to population growth is habitat-specific. These results provide new information about the ecology of migratory species and also demonstrate the importance of considering both temporal and spatial drivers of population dynamics.



**Figure 3.4** Posterior distributions of the proportional contribution of (a) fecundity, (b) immigration, (c) recruitment, and (d) adult survival to plot-level annual population growth for Wood Thrush breeding in southern Indiana, USA. For each demographic rate, the white line indicates the posterior mean and the dark grey and light grey areas indicate the 50% and 95% highest posterior density intervals, respectively. Plots are ranked on the y-axis by their self-recruitment rate ( $R$ ), which is strongly correlated with a key proxy of habitat quality for Wood Thrush.

Although estimates of spring and autumn migration survival exist for several larger species that are hunted or can carry satellite transmitters (Ward et al. 1997; Klaassen et al. 2014; Lok et al. 2015), mortality within these stages remain relatively unknown for smaller-bodied species. Previous analyses of resighting data from one songbird species indicates that mortality appears to be concentrated in the migratory stages (Sillett & Holmes 2002), but this study was not designed to separate autumn from spring mortality. Our integrated approach enabled us to use mark-resight data to produce the first separate survival estimates for spring and autumn migration for a migratory passerine. For Wood Thrush, the migratory stages of the annual cycle accounted for the highest mortality among both adult and juvenile age-classes; however, spring was riskier than fall migration. Interestingly, the proportion of mortality during the migratory periods was similar to that of several larger-bodied bird species that have been tracked using satellite transmitters.

Klaassen et al. (2014) found that the migratory periods accounted for 55% of overall mortality and that survival was ~8% lower in spring than autumn for Osprey (*Pandion haliaetus*), Marsh Harriers (*Circus aeruginosus*), and Montagu's Harriers (*Circus pygargus*). Similarly, Lok et al. (2015) found that survival during spring migration was ~16% lower in spring than autumn for Eurasian Spoonbills (*Platalea leucorodia leucorodia*). Collectively, these results suggest that high mortality during spring migration may be a general phenomenon across many migratory birds. As direct and indirect methods to quantify migration survival continue to improve, phylogenetic contrasts across taxa that vary in body size and life-history strategies will offer important insights into the ecology of migratory species.

The ability to separately estimate apparent survival during spring and autumn migration is particularly important given the differential contribution of these vital rates to population dynamics. Juvenile and adult spring migration survival had the largest contributions to population growth, cumulatively accounting for ~38% of the variation in  $\lambda$ . The importance of spring migration survival to the population dynamics of a migratory bird has not previously been shown directly, but past research on the ecology of migratory birds support our results. First, most species of Neotropical migratory birds depart their tropical wintering grounds on spring migration when precipitation and insect abundance are at their annual nadir (Janzen 1973). The scarcity of food resources during this stage limits the ability of individuals to build fat reserves prior to migration (Studds & Marra 2007) and makes them more susceptible to adverse conditions experienced during migration (Finch et al. 2014). Second, because reproductive success is strongly tied to early arrival on the breeding grounds (Lozano et al. 1996), individuals are under severe time constraints during spring migration (Kokko 1999). Numerous empirical studies have shown that individuals migrate faster in spring than in autumn (Stutchbury et al. 2009; Tøttrup et al. 2011; Nilsson et al. 2013) and the urgency to reach the breeding grounds may further limit the ability of individuals to rest and refuel en route. Viewed cumulatively, our results combined with those from other studies on migratory birds, implicate spring migration as a critical period of the annual cycle in which significant mortality occurs. More work is needed to corroborate our findings in additional species.

Although our integrated population model provides a novel method for estimating stage-specific survival from re-sighting data, our survival estimates may be biased low by permanent emigration of individuals from the study plots. The similarity between our estimates of adult migration survival and estimates from satellite tracking (Klaassen et al. 2014; Lok et al. 2015) suggests that permanent emigration of adults (i.e., breeding dispersal) may not have been a major source of bias in our data. However, extensive natal dispersal may have biased our estimates of spring migration survival for first-year birds, especially in low-quality breeding habitats (Anders & Marshall 2005). As a result, we were unable to determine whether the low survival of juveniles during spring migration is the result of low true survival, high natal dispersal, or a combination of the two. If extensive natal dispersal contributed to the low estimates of spring migration survival, then annual variation in dispersal (Rushing et al. 2015) may also explain the contribution of this period to variation in population growth. Ultimately, habitat- and season-specific natal dispersal probabilities will be required to fully account for permanent emigration and reduce bias in juvenile survival estimation (Gilroy et al. 2012).

Although survival during spring migration had the largest stage-specific contribution to  $\lambda$ , vital rates during the breeding season (adult survival, fecundity, and post-fledging survival) cumulatively accounted for nearly as much variation (37%; Table 1). This finding emphasizes the importance of breeding season limitation compared to other portions of the annual cycle for Wood Thrush as found by Rushing et al. (Rushing et al. 2016a, b) and corroborates similar patterns

documented for a number of migratory bird populations (Newton 2004). In addition, our results also emphasize that spatial variation in breeding habitat quality influences the contribution of vital rates to variance in  $\lambda$ . Environmental heterogeneity and habitat-specific demography have long been hypothesized to be central to spatial variation in population growth (Holt 1984; Pulliam 1988; Dias 1996; Hanski 1999), yet our results highlight a subtle, but important extension. We show that the relative contribution of vital rates to  $\lambda$  varies significantly among habitats that differ in quality. Recruitment and fecundity contribute more to  $\lambda$  in high-quality habitats, whereas adult survival contributes more to  $\lambda$  in lower quality habitats. We hypothesize that these results are driven primarily by high permanent emigration of adults in low-quality plots following reproductive failure (Part & Gustafsson 1989; Haas 1998). In contrast, low emigration of adults from high-quality plots increases the relative importance of fecundity and recruitment. Given that fecundity can contribute substantially to variance in  $\lambda$ , especially in high-quality plots, our results underscore the need to accurately account for total annual reproductive effort (i.e., rebreeding or multiple brooding; Etterson et al. 2009; Sim et al. 2011). Failure to include rebreeding in our model would have biased fecundity estimates by -40% and thus underestimated the contribution of breeding season factors to  $\lambda$  and masked conclusions about the relative importance of fecundity to population persistence across heterogeneous habitats.

Our results also indicate that the contribution of immigration to population dynamics was scale-dependent. At the regional scale, annual variation in immigration had a small contribution to variation in  $\lambda$ , despite a relatively high overall immigration rate (Table 1). At the plot-scale, however, the contribution of immigration was large (range: 0.09-0.49; mean = 0.22; Table 1) and in some cases greater than the contributions of other vital rates (Fig. 4). These results are consistent with theoretical predictions that the emigration and immigration of individuals from a population can be comparable to births and deaths at local scales, but are largely redistribution processes at regional scales (Camus & Lima 2002). Despite the contribution of immigration to  $\lambda$  at the plot-level, we found no evidence that immigration explained a larger portion of the variance in population growth in high-quality versus low-quality habitats. This result is contrary to the predictions of source-sink theory (Pulliam 1988; but see Gundersen et al. 2001) and suggests predicting the dynamics of source-sink populations requires measuring the contribution of immigration, not simply differences in the immigration rate.

Survival of adults and juveniles during winter and autumn migration collectively account for only ~12% of the variation in  $\lambda$ , but our estimates of the direct contribution of these stages may underestimate their influence on population dynamics for several reasons. First, many Wood Thrush move within the stationary winter period and the presence of transient individuals can have complex effects on population dynamics (Penteriani et al. 2011). Unfortunately, we were unable to estimate the survival of these transient individuals from our mark-recapture data and therefore could not account for their influence on  $\lambda$ . If these transient individuals experience lower or more variable survival, the true contribution of overwinter survival to  $\lambda$  may be larger than our results indicate. Second, a growing body of research has revealed the ubiquitous nature of seasonal interactions in migratory species, namely carry-over effects (Harrison et al. 2011). Biotic or abiotic conditions experienced during autumn or winter may be important in limiting Wood Thrush populations via indirect effects on spring migration survival and/or fecundity (Wilson et al. 2011). Accounting for carry-over effects would not change our estimates of vital rate contribution to  $\lambda$ ; nevertheless, determining the ultimate factors that determine variation in demographic rates is needed to develop management strategies that target limiting factors. Unfortunately, little is known about the causes of migration mortality in songbirds. Our full-annual-cycle IPM provides a

framework for exploring the relative importance of carry-over effects (e.g., winter habitat quality) versus within-season factors (e.g., weather, availability of stopover habitat, collisions), for example by including hypothesized drivers of migration survival as covariates in the model. Progress on this subject requires long-term data that enable estimates of stage-specific density dependence (Betini et al. 2013; Robinson et al. 2016a) and the strength of covariance between environmental factors in one season and fitness during subsequent stages (Harrison et al. 2011). Collectively, our results highlight the important contribution of the migratory stage to population dynamics and underscore the need to further understand the stage-specific and/or carry-over mechanisms that limit migration survival (Clausen et al. 2015; Paxton & Moore 2015; Hewson et al. 2016).

Effective conservation of globally declining migratory species (Wilcove & Wikelski 2008) requires a firm understanding of when and where populations are limited. Historically, studies of population limitation have rarely been replicated across heterogeneous habitats (Pearson & Fraterrigo 2011) and have focused solely on the breeding period (Marra et al. 2015). Collectively, researchers have tended to ignore spatial variation in population dynamics (Rushing et al. 2016b) and the role of demographic processes operating during the non-breeding stages (Anteau & Afton 2004; Baker et al. 2004; Hewson et al. 2016). In this paper, we provide an IPM framework that allows quantifying stage- and habitat-specific vital rates and their contribution to population dynamics. Given the flexibility of IPMs to accommodate multiple types of data and sub-model structure, continued development of this full-annual-cycle framework will enhance our understanding and conservation of migratory animals. For example, this framework could also be useful for comparative (intra- and inter-specific) demographic analyses and for testing predictions of life-history theory (Alerstam et al. 2003). Ultimately, we believe this analytical framework will advance the field of population ecology by helping to identify when and where populations are limited, determining how biotic and abiotic processes influence demographic rates, and predicting the consequences of environmental change or management strategies.

## **Conclusions and Implications for Future Research**

These results underscore the importance of understanding how spatial and temporal variation in vital rates contribute to population dynamics. Previous empirical work largely identified sources and sinks based on single site studies that failed to account for how vital rates change across the annual cycle. Our results highlight that migration may be a critical phase of the annual cycle for Wood thrush population dynamics. The development of this full-annual cycle model should be broadly applicable across migratory birds and can identify when during the annual cycle species of concern may be limited. Although our results do underscore the importance of the migratory period, they also show clearly that breeding season processes account for the vast majority of variation in population growth. Understanding that Wood thrush populations are largely breeding season limited is essential for making proactive conservation decisions. This result further highlights that managers can make positive impacts on species of concern through habitat management approaches that can maximize survival, recruitment, and fecundity. Our results also show that habitat specific demography contributes to spatial variation in source sink dynamics in previously unforeseen ways. Specifically, our results show that vital rates make differential contributions to population growth depending on the quality of the habitat. This suggests that managing populations for persistence, via increasing specific vital rates, may need to be done in a habitat-specific manner. Moreover, while our results clearly show that immigration is still key to rescuing sink populations, immigration may not always be high in locations with  $\lambda$  below

one. Given that our integrated model estimates immigration as a latent variable future work will be needed to compare our model estimates with those derived from other sources (i.e., isotope data). Isotope analyses are part of our SERDP grant and while the results were not explicitly presented in this report, we are actively working on this element of the research. In contrast to immigration, our ability to estimate emigration or understand its relative contribution to source-sink dynamics remains a key weakness of the integrated population model approach. Demographic modeling has long struggled with the issues of separating permanent emigration from true mortality and this remains a key focus of future research. Recent analytical advances, such as spatial mark-recapture are one of the few methods that estimate true survival and differentiate mortality from emigration (within and between seasons). We collected the requisite data to build these models and while not part of the scope of the current project, these results will provide added value for our understanding of avian population dynamics. Future analyses will include spatial mark-recapture analyses with the Wood thrush dataset. Although our model and results have largely focused on the proximate drivers of population dynamics, future research must examine the ultimate mechanisms that shape demography. We are currently working on extending our integrated population model to examine how both local habitat and landscape configuration influence both vital rates of interest and source-sink dynamics. Likewise, our analyses highlight which vital rates are particularly important for Wood thrush populations on DoD installations and future work to better understand how these rates co-vary with environmental heterogeneity will be essential to create informed management practices. To these ends, we are currently working on detailed analyses of key factors that influence Wood thrush adult survival, recruitment and fecundity.

### Literature Cited

- Alerstam, T., Hedenstrom, A. & Akesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103**, 247–260.
- Anders, A.D. & Marshall, M.R. (2005) Increasing the accuracy of productivity and survival estimates in assessing landbird population status. *Conserv. Biol.*, **19**, 66–74.
- Anteau, M.J. & Afton, A.D. (2004) Nutrient reserves of Lesser Scaup (*Aythya affinis*) during spring migration in the Mississippi flyway: a test of the spring condition hypothesis. *The Auk*, **121**, 917–929.
- Baker, A.J., Gonzalez, P.M., Piersma, T., Niles, L.J., de Lima Serrano do Nascimento, I., Atkinson, P.W., et al. (2004) Rapid population decline in Red Knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. *Proc. R. Soc. B Biol. Sci.*, **271**, 875–882.
- Betini, G.S., Griswold, C.K. & Norris, D.R. (2013) Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment. *Proc. R. Soc. Lond. B Biol. Sci.*, **280**, 20130110.
- Camus, P.A. & Lima, M. (2002) Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population concepts. *Oikos*, **97**, 433–438.
- Caswell, H. (2001) *Matrix Population Models*. Sinauer Associates, Sunderland, MA, USA
- Chandler, R.B. & Clark, J.D. (2014). Spatially explicit integrated population models. *Methods Ecol. Evol.*, **5**, 1351–1360.
- Clausen, K.K., Madsen, J. & Tombre, I.M. (2015) Carry-over or compensation? The impact of winter harshness and post-winter body condition on spring-fattening in a migratory goose species. *PloS One*, **10**, e0132312.
- Dias, P.C. (1996). Sources and sinks in population biology. *Trends Ecol. Evol.*, **11**, 326–330.



- Diez, J.M. & Giladi, I. (2011) Scale-dependence of habitat sources and sinks. In: *Sources, Sinks and Sustainability* (eds. Liu, J., Hull, V., Morzillo, A. & Wiens, J.). Cambridge University Press, Cambridge, UK, pp. 1–26.
- Etterson, M.A., Bennett, R.S., Kershner, E.L. & Walk, J.W. (2009) Markov chain estimation of avian seasonal fecundity. *Ecol. Appl.*, **19**, 622–630.
- Finch, T., Pearce-Higgins, J.W., Leech, D.I. & Evans, K.L. (2014) Carry-over effects from passage regions are more important than breeding climate in determining the breeding phenology and performance of three avian migrants of conservation concern. *Biodivers. Conserv.*, **23**, 2427–2444.
- Getz, L.L., Oli, M.K., Hofmann, J.E. & McGuire, B. (2005) Habitat-Specific Demography of Sympatric Vole Populations over 25 Years. *J. Mammal.*, **86**, 561–568.
- Gilroy, J.J., Virzi, T., Boulton, R.L. & Lockwood, J.L. (2012) A new approach to the “apparent survival” problem: estimating true survival rates from mark–recapture studies. *Ecology*, **93**, 1509–1516.
- Gundersen, G., Johannesen, E., Andreassen, H. p. & Ims, R. a. (2001) Source–sink dynamics: how sinks affect demography of sources. *Ecol. Lett.*, **4**, 14–21.
- Haas, C.A. (1998) Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. *The Auk*, **115**, 929–936.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, Oxford, UK.
- Harrison, X.A., Blount, J.D., Inger, R., Norris, D.R. & Bearhop, S. (2011) Carry-over effects as drivers of fitness differences in animals. *J. Anim. Ecol.*, **80**, 4–18.
- Hewson, C.M., Thorup, K., Pearce-Higgins, J.W. & Atkinson, P.W. (2016) Population decline is linked to migration route in the Common Cuckoo. *Nat. Commun.*, **7**, 12296.
- Holmes, R.T., Marra, P.P. & Sherry, T.W. (1996) Habitat-specific demography of breeding Black-Throated Blue Warblers (*Dendroica caerulescens*): Implications for population dynamics. *J. Anim. Ecol.*, **65**, 183–195.
- Holt, R.D. (1984) Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.*, **124**, 377–406.
- Hostetler, J.A., Sillett, T.S. & Marra, P.P. (2015) Full-annual-cycle population models for migratory birds. *The Auk*, **132**, 433–449.
- Janzen, D.H. (1973) Sweep samples of tropical foliage insects: Effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology*, **54**, 687–708.
- Kellner, K. (2016) *jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses*.
- Kéry, M. & Schaub, M. (2012) *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*. Academic Press, Waltham, MA, USA.
- Klaassen, R.H.G., Hake, M., Strandberg, R., Koks, B.J., Trierweiler, C., Exo, K.-M., et al. (2014) When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *J. Anim. Ecol.*, **83**, 176–184.
- Kokko, H. (1999) Competition for early arrival in migratory birds. *J. Anim. Ecol.*, **68**, 940–950.
- Kreuzer, M.P. & Huntly, N.J. (2003) Habitat-specific demography: evidence for source-sink population structure in a mammal, the pika. *Oecologia*, **134**, 343–349.
- Lok, T., Overdijk, O. & Piersma, T. (2015) The cost of migration: spoonbills suffer higher mortality during trans-Saharan spring migrations only. *Biol. Lett.*, **11**, 20140944.
- Lozano, G.A., Perreault, S. & Lemon, R.E. (1996) Age, arrival date and reproductive success of male American Redstarts *Setophaga ruticilla*. *J. Avian Biol.*, **27**, 164–170.



- Marra, P.P., Cohen, E.B., Loss, S.R., Rutter, J.E. & Tonra, C.M. (2015) A call for full annual cycle research in animal ecology. *Biol. Lett.*, **11**, 20150552.
- Mattsson, B.J., Runge, M.C., Devries, J.H., Boomer, G.S., Eadie, J.M., Haukos, D.A., et al. (2012) A modeling framework for integrated harvest and habitat management of North American waterfowl: Case-study of Northern Pintail metapopulation dynamics. *Ecol. Model.*, **225**, 146–158.
- Murphy, M.T. (2001) Habitat-specific demography of a long-distance, Neotropical migrant bird, the Eastern Kingbird. *Ecology*, **82**, 1304–1318.
- Newton, I. (2004) Population limitation in migrants: Population limitation in migrants. *Ibis*, **146**, 197–226.
- Nichols, J.D. (1996) Sources of variation in migratory movements of animal populations: statistical inference and a selective review of empirical results for birds. In: *Population Dynamics in Ecological Space and Time* (eds. Rhodes, O.E., Chesser, R.K. & Smith, M.H.). University of Chicago Press, Chicago, IL, pp. 147–197.
- Nilsson, C., Klaassen, R.H.G. & Alerstam, T. (2013) Differences in Speed and Duration of Bird Migration between Spring and Autumn. *Am. Nat.*, **181**, 837–845.
- Norman, D. & Peach, W.J. (2013) Density-dependent survival and recruitment in a long-distance Palaearctic migrant, the Sand Martin *Riparia riparia*. *Ibis*, **155**, 284–296.
- Oro, D. (2013) Grand challenges in population dynamics. *Front. Ecol. Evol.*, **1**, 1–2.
- Part, T. & Gustafsson, L. (1989) Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): Possible causes and reproductive consequences. *J. Anim. Ecol.*, **58**, 305–320.
- Paxton, K.L. & Moore, F.R. (2015) Carry-over effects of winter habitat quality on en route timing and condition of a migratory passerine during spring migration. *J. Avian Biol.*, **46**, 495–506.
- Pearson, S. & Fraterrigo, J. (2011) Habitat quality, niche breadth, temporal stochasticity, and the persistence of populations in heterogeneous landscapes. In: *Sources, Sinks, and Sustainability* (eds. Liu, J., Hull, V., Morzillo, A. & Wiens, J.). Cambridge University Press, Cambridge, UK.
- Penteriani, V., Ferrer, M. & Delgado, M.M. (2011) Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. *Anim. Conserv.*, **14**, 233–241.
- Pereira, J.A. & Novaro, A.J. (2014) Habitat-specific demography and conservation of Geoffroy's cats in a human-dominated landscape. *J. Mammal.*, **95**, 1025–1035.
- Plummer, M. (2003) *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*.
- Pradel, R., Hines, J.E., Lebreton, J.-D. & Nichols, J.D. (1997) Capture-Recapture Survival Models Taking Account of Transients. *Biometrics*, **53**, 60–72.
- Pulliam, H.R. (1988) Sources, Sinks, and Population Regulation. *Am. Nat.*, **132**, 652–661.
- Pulliam, H.R. (1996) Sources and Sinks: Empirical evidence and population consequences. In: *Population Dynamics in Ecological Space and Time* (eds. Rhodes, O.E., Chesser, R.K. & Smith, M.H.). University of Chicago Press, Chicago, IL, pp. 45–69.
- R Development Core Team. (2015) *R: A Language and Environment for Statistical Computing*. Vienna, Austria.
- Rhodes, J.R., Ng, C.F., de Villiers, D.L., Preece, H.J., McAlpine, C.A. & Possingham, H.P. (2011) Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biol. Conserv.*, The New Conservation Debate: Beyond Parks vs. People, **144**, 1081–1088.

- Robinson, O.J., McGowan, C.P. & Devers, P.K. (2016a) Disentangling density dependent dynamics using full annual cycle models and Bayesian model weight updating. *J. Appl. Ecol.*
- Robinson, O.J., McGowan, C.P., Devers, P.K., Brook, R.W., Huang, M., Jones, M., et al. (2016b) A full annual cycle modeling framework for American Black Ducks. *Nat. Resour. Model.*, **29**, 159–174.
- Robinson, R.A., Morrison, C.A. & Baillie, S.R. (2014) Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. *Methods Ecol. Evol.*, **5**, 1361–1372.
- Runge, J.P., Runge, M.C., Nichols, J.D., Stamps, A.E.J.A. & DeAngelis, E.D.L. (2006) The Role of Local Populations within a Landscape Context: Defining and Classifying Sources and Sinks. *Am. Nat.*, **167**, 925–938.
- Runge, M.C. & Marra, P.P. (2005) Modeling seasonal interactions in the population dynamics of migratory birds. In: *Birds of two worlds: the ecology and evolution of migration* (eds. Greenberg, R. & Marra, P.P.). Johns Hopkins University Press, Baltimore, MD, pp. 375–389.
- Rushing, C.S., Dudash, M.R., Studds, C.E. & Marra, P.P. (2015) Annual variation in long-distance dispersal driven by breeding and non-breeding season climatic conditions in a migratory bird. *Ecography*, **38**, 1006–1014.
- Rushing, C.S., Ryder, T.B. & Marra, P.P. (2016a) Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc R Soc B*, **283**, 20152846.
- Rushing, C.S., Ryder, T.B., Scarpignato, A.L., Saracco, J.F. & Marra, P.P. (2016b) Using demographic attributes from long-term monitoring data to delineate natural population structure. *J. Appl. Ecol.*, **53**, 491–500.
- Sæther, B.-E. & Bakke, Ø. (2000) Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, **81**, 642–653.
- Schaub, M. & Abadi, F. (2010) Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.*, **152**, 227–237.
- Schaub, M., Gimenez, O., Sierro, A. & Arlettaz, R. (2007) Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. *Conserv. Biol.*, **21**, 945–955.
- Sherry, T.E. & Holmes, R.T. (1995) Summer versus winter limitation of populations: what are the issues and what is the evidence? In: *Ecology and Management of Neotropical Migratory Birds: A Synthesis and Review of Critical Issues* (eds. Martin, T.E. & Finch, D.M.). Oxford University Press, Oxford, UK.
- Sillett, T.S. & Holmes, R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.*, **71**, 296–308.
- Sim, I.M.W., Rebecca, G.W., Ludwig, S.C., Grant, M.C. & Reid, J.M. (2011) Characterizing demographic variation and contributions to population growth rate in a declining population. *J. Anim. Ecol.*, **80**, 159–170.
- Stanley, C.Q., McKinnon, E.A., Fraser, K.C., Macpherson, M.P., Casbourn, G., Friesen, L., et al. (2015) Connectivity of wood thrush breeding, wintering, and migration sites based on range-wide tracking: Wood Thrush Migration Networks. *Conserv. Biol.*, **29**, 164–174.
- Studds, C. & Marra, P. (2007) Linking fluctuations in rainfall to nonbreeding season performance in a long-distance migratory bird, *Setophaga ruticilla*. *Clim. Res.*, **35**, 115–122.
- Stutchbury, B.J.M., Tarof, S.A., Done, T., Gow, E., Kramer, P.M., Tautin, J., et al. (2009) Tracking long-distance songbird migration by using geolocators. *Science*, **323**, 896–896.
- Sutherland, W.J. (1996) Predicting the consequences of habitat loss for migratory populations. *Proc. Biol. Sci.*, **263**, 1325–1327.

- Taylor, C.M. & Stutchbury, B.J.M. (2016) Effects of breeding versus winter habitat loss and fragmentation on the population dynamics of a migratory songbird. *Ecol. Appl. Publ. Ecol. Soc. Am.*, **26**, 424–437.
- Tøttrup, A.P., Klaassen, R.H.G., Strandberg, R., Thorup, K., Kristensen, M.W., Jørgensen, P.S., et al. (2012) The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proc. R. Soc. Lond. B Biol. Sci.*, **279**, 1008–1016.
- Ward, D.H., Rexstad, E.A., Sedinger, J.S., Lindberg, M.S. & Dawe, N.K. (1997) Seasonal and annual survival of adult Pacific Brant. *J. Wildl. Manag.*, **61**, 773–781.
- Weegman, M.D., Bearhop, S., Fox, A.D., Hilton, G.M., Walsh, A.J., McDonald, J.L., et al. (2016) Integrated population modelling reveals a perceived source to be a cryptic sink. *J. Anim. Ecol.*, **85**, 467–475.
- Wilcove, D.S. & Wikelski, M. (2008) Going, Going, Gone: Is animal migration disappearing. *PLoS Biol.*, **6**, e188.
- Wilson, S., LaDeau, S.L., Tøttrup, A.P. & Marra, P.P. (2011) Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology*, **92**, 1789–1798.

## **Chapter 4- Synthesizing what different methodological approaches tell us about avian demography on Department of Defense installations**

### **Abstract**

The spatial distribution and temporal stability of animal populations is a function of habitat quality, habitat selection, and dispersal. Source-sink dynamics – how local and regional processes structure populations and influence their persistence – comprise an essential aspect of population stability. Multiple methods are available to investigate source-sink dynamics in avian populations, each varying in degree of effort and expense. The Department of Defense (DoD), which manages nearly 25 million acres of high-value bird habitat, primarily uses the Monitoring Avian Productivity and Survivorship (MAPS) protocol to monitor avian populations and inform the management of bird species on its properties. However, the value of MAPS for quantifying avian source-sink dynamics at both local and regional scales has never been rigorously assessed or validated. Likewise, other more cost-effective avian sampling approaches, such as point counts, can produce accurate abundance estimates. Although improved analytical approaches have made count-based abundance data useful for estimating vital rates and to model population growth, these approaches are not widely used on DoD installations for assessing population change and/or health. To date, no study has validated or tested the efficacy of these three approaches for identifying sources and sinks, despite this information being essential for making proactive management decisions on DoD properties. Our results show that each method produced differing estimates of population growth with low concordance among sites being classified as sources/sinks. The uniform identification of sources across methods was true only for highest quality habitats (e.g., unmanaged large tracts of forest at BONWR), whereas in fragmented or managed habitats (e.g., Crane and Indiana Department of Natural Resource properties), estimates were more variable and often showed little correspondence. When comparing across techniques, we find a correlation between point-count based and intensive demographic estimates of population growth. In contrast, we see low correlation between MAPS based estimates of lambda and those derived from count and demographic data. Despite a correlation between point count and demographic estimates of lambda, these approaches often came to different conclusions about a site being source vs. sink. Viewed broadly, our results suggest the methodological approach chosen for sampling avian populations will be dependent upon the scale at which management decisions need to be made. In higher quality habitats or at larger spatial scales, some species of concern may be monitored with less expensive count based and MAPS approaches, however, in lower quality habitat or smaller spatial temporal demographic stochasticity will require the more detailed intensive demographic approach. Examination of the predictors of local population growth show that local habitat was the best predictor of self-recruitment rate, although models containing patch size and forest cover within 2 km also received some support. Specifically, forest structure, as measured by the number of trees with greater than 30 centimeters' diameter breast height, was a very strong predictor of high quality source Wood thrush habitat. As such, habitat management recommendations for Wood thrush will require growth and retention of large trees as well as the encouragement of heterogeneous vertical foliage structure and understory shrub cover for nesting habitat. Finally, a comparison of occupancy (distributional patterns) and demographic data suggest that although count data are less precise when it comes to understanding species-specific demography, they can be used as a heuristic tool. Specifically, congruence between the occupancy results and the key drivers of self-recruitment rate for Wood thrush suggest that count data can be an indicator of demographic performance for a broader suite of interior forest birds.

## Objective

Here, we synthesize the results from the three methodological approaches reported on in Chapters 1-3 to determine the most cost-effective tools for monitoring avian population dynamics and developing subsequent management strategies for avian species of concern. First, we examine Wood thrush (*Hylocichla mustelina*) population growth estimates ( $\lambda$ ) as derived from MAPS data, point count data, and intensive demographic data. We specifically estimated population growth from each data source using N-mixture models, Pradel models and integrated population models, respectively. Intensive demographic monitoring is widely accepted as the most reliable method of estimating population growth rates (Kendall & Nichols 2004), and in comparing these estimates to those derived from point count and banding only (MAPS) data, we can quantify the accuracy and precision of these less labor intensive methods for characterizing avian population dynamics. Second, we examine the local and landscape predictors of self-recruitment rate for the intensive demographic data. Third, we examine issues of spatial scale to assess if different methodological approaches are useful for making prescriptive local vs. landscape management decisions. Finally, we compare the results from the occupancy modeling and demographic monitoring to broadly discuss the relationships between distributional patterns and population dynamics for a suite of passerine species on DoD installations.

## Background

One of the most studied and publicized conservation issues of the past 25 years is the decline of Nearctic-Neotropical migratory bird populations (e.g., Robbins et al. 1989; James et al. 1996; Sauer & Link 2002; Lloyd-Evans and Atwood 2004). Understanding the causes of these declines requires information about the factors that limit population growth year round, including reproductive success, survivorship, and habitat suitability (Sherry & Holmes 1995; Sillett & Holmes 2002). The management of Neotropical-Nearctic migratory birds is a conservation priority for the DoD. Much of the 30 million acres of DoD land serves as critical bird habitat and supports significant populations of avian species of concern (SOC). The importance of DoD installations for populations of migratory birds is underscored by the categorization of several bases as Important Bird Areas (including Crane Naval Surface Warfare Center and Big Oaks National Wildlife Refuge) that sustain healthy populations of forest-breeding Neotropical migrants of conservation concern (Nott & Morris 2007).

Over the last two decades, the DoD has met the challenge of carrying out its mission while simultaneously complying with environmental laws and regulations. The Bob Stump National Defense Authorization Act for FY 2003 (Incidental Take of Migratory Birds During Military Readiness Activities) provided temporary legislative relief to the DoD by exempting military readiness activities (MRAs) from incidental take under the Migratory Bird Treaty Act (MBTA). Until recently, the MBTA focused on the direct and intentional take of migratory birds, but now the legislation prohibits both unpermitted “intentional” and “unintentional” take, including take that occurs as a result of military training and operations. In 2007, the DoD/Migratory Bird Rule established the conditions requiring that DoD cooperate with the USFWS if proposed or ongoing Military Readiness Activities were to result in significant adverse effects on populations of migratory birds. The USFWS can withdraw take authorization if conservation measures or required monitoring efforts have not been implemented. More recently, DoD wildlife managers have outlined a strategic bird-monitoring plan to promote management of migratory species in concert with the military mission (Bart et al. 2010).



Effective management of migratory birds requires unbiased estimates of demographic parameters (i.e., stage-specific survival and fecundity) within the context of the annual cycle, as well as predictions of how land management changes could influence these vital rates (Noon & Sauer 1992; Larson et al. 2004) and thus shape population structure and subsequent persistence. Although studies have investigated relationships between regional landscape patterns and population trends (e.g., Flather & Sauer 1996; Sauer et al. 1996), few have examined the relationship between landscape configuration and vital rates at multiple spatial and temporal scales (Villard et al. 1999). To be successful, management actions must be designed to influence the key demographic parameters responsible for population decline in a specific target species (DeSante 1995).

The concepts of source-sink dynamics are well integrated into ecological theory, and a large number of studies on vertebrates have aimed to categorize populations as sources or sinks (Runge et al. 2006). This research, much of it with birds, has used a variety of approaches to differentiate sources from sinks. Moreover, these approaches vary widely in the effort required and data sources used to determine population growth trajectories and persistence probabilities. Some studies have quantified basic measures of presence-absence to model dynamics in patch occupancy (Betts et al. 2008; Kery & Royle 2010). Others have quantified attributes of site-specific demography (reproductive success, adult survival and both apparent and simulated juvenile survival) to categorize populations (e.g., Donovan et al. 1995; Vierling 2000; Fauth 2001). Fewer studies, however, have taken a more biologically realistic approach by incorporating rates of immigration and emigration within focal subpopulations (e.g., Breininger et al. 1995; Hatchwell et al. 1996; Mumme et al. 2000). Finally, few studies measure the per capita contribution that each member of the focal subpopulation makes to the greater meta-population (Donacaster et al. 1997).

Although direct measurement of per capita survival, annual fecundity, and dispersal is the most unbiased and accurate method for categorizing sites as sources or sinks, this approach is labor-intensive and costly, and thus rarely used with birds (Webster et al. 2002; Kendall & Nichols 2004). Alternate estimates of vital rates and population persistence can be used to indirectly provide information on source sink dynamics. The most widespread tool used to estimate vital rates of bird populations in the continental US is MAPS (Desante et al. 1995) and is the only program that collects data at the scales needed for assessing regional population dynamics. MAPS generates indices of breeding productivity and estimates of density and apparent survival rates, but its power to quantify source-sink dynamics remains to be tested. For example, annual estimates of density (local variation in population size) may be masked or accentuated by region-wide immigration and emigration (DeSante 1990; George et al. 1992) such that density alone may not indicate population viability (Van Horne 1983; Pulliam 1988; Donovan et al. 1995). In addition, while MAPS provides essential estimates of site-specific adult survival, this only represents a single age class during one part of the annual cycle: the breeding season. Moreover, the accuracy of the MAPS index of breeding productivity for estimating reproductive success at the relevant and site-specific scale has not been rigorously validated.

Estimation of patch-level changes in population size may be used to indirectly categorize source and sink areas (Hanski & Ovaskainen 2000; Pulliam & Danielson 1991; Betts et al. 2008). Avian point count data and dynamic N-mixture models (Dail & Madsen 2011) have been used to test for changes in abundance, recruitment, and apparent survival among sites within and between breeding seasons. These dynamic models account for biases in site abundance and movement caused by imperfect detectability, a ubiquitous feature of bird surveys (Alldredge et al. 2007; Zhou & Griffiths 2007), and by constraining rates of gains and losses as a single parameter, one can



estimate site or patch level growth rates (Dail & Madsen 2011). Recent evidence suggests that sites with high passerine survival and reproduction (i.e., putative sources) can be identified using such point count models (e.g., Betts et al. 2008). These methods are thus increasingly appealing for conservation biologists and landscape managers given the costs associated with collecting detailed demographic data (Hurme et al. 2008; Rota et al. 2009). However, no studies have directly tested the predictions of dynamic N-mixture models in relation to either comprehensive demographic data or to survival and reproductive index data collected from MAPS.

To effectively manage natural populations, demographic data from source and sink sites must also be linked with information about the distribution and size of habitat patches in the landscape. A number of studies have documented the effect of habitat amount, patch size, and connectivity on the viability of local populations in fragmented landscapes (e.g., Robinson et al. 1995; Hoover et al. 1995; Donovan et al. 1995). Specifically, recent work on DoD installations in the Midwest indicates that forest amount is often a good predictor of demographic performance measures for a number of Neotropical migrant birds (Nott & Morris 2007). Despite some empirical work we still lack an understanding of which aspect of landscape structure are most critical to avian population persistence, and how habitat quality shapes the per capita contribution of local populations to regional metapopulations.

## Methods

Here, we outline the estimation of population growth ( $\lambda$ ) for the three avian sampling techniques that vary in unit effort and data resolution. We define sources as sites that have positive population growth ( $\lambda > 1$ ) and sinks as sites in demographic deficit ( $\lambda < 1$ ). Importantly, these designations cannot explicitly account for the role of immigration such that a site may be designated as a source, but the vital rates would not be sufficient for site persistence in the absence of immigration. As such, we review the importance of self-recruitment rate and its drivers to best understand both site persistence and the relative contributions that each subpopulation makes to regional population dynamics.

### Point-Count N-mixture Models

To estimate plot-specific population growth rates from the point count data ( $\lambda_{PC}$ ), we used all information collected at all 683 point count stations. Prior to modeling, we removed all detections of individuals that were recorded greater than 50 m from any point count station, and counted the remaining Wood Thrush detections during each 10 minute sample visit. Results from our tests of closure violations in Chapter 1 indicated that it is reasonable to assume superpopulation closure within a single breeding season for Wood Thrush, and thus we fit a dynamic N-mixture model to the dataset (Dail & Madsen 2011). All repeated visits to a site within a breeding season were considered part of the same primary period, and visits within a breeding season were treated as secondary periods. The model was fit using the `pcountOpen()` function in the R package “unmarked.” Superpopulation size at site  $i$  during primary period  $t$  ( $N_{it}$ ) was assumed to follow a negative binomial distribution, and using the `dynamics = “trend”` option, we specified that  $E(N_{it}) = E(N_{it-1}) * \lambda_i$ . Under this model specification,  $\lambda_i$  represents the estimated inter-annual growth rate at site  $i$ . We included time of day and Julian date as covariates for detection probability in the model, and demographic plot as a covariate for both initial site abundance ( $N_{i1}$ ), and growth rate ( $\lambda_i$ ). The 490 point count stations that were not located on a demographic plot were lumped into

a single category. We report plot-specific estimated growth rate values for comparison with the other data collection techniques.

### MAPS Population Growth Rate Estimation

We applied Pradel reverse-time capture-mark-recapture models (Pradel, 1996) to MAPS data to estimate time-constant annual population growth rate ( $\lambda_{\text{MAPS}}$ ) at each station. We implemented the model using the ‘ $\lambda$  and  $\phi$ ’ parameterization in program MARK (White & Burnham, 1999). We ran program MARK in R (R Core Team, 2015) using the RMark package (Laake, 2013). We included fixed plot (station) effects for models of both apparent survival ( $\phi$ ) and population growth ( $\lambda$ ). As for our CJS models, we modeled recapture probability ( $p$ ) as a logit-linear function of a station-specific covariate representing the mean number of times individuals were captured at the station per season (Saracco, Desante, & Kaschube, 2008).

### Intensive Demographic Population Growth Rate

Estimates of population growth for the intensive demographic data ( $\lambda_{\text{ID}}$ ) were derived from the integrated population modeling framework (see Appendix A for parameter estimate details). For each plot, annual population growth rates were approximated as:

$$\lambda_{p,t} = \frac{n_{p,t}}{n_{p,t-1}} = f_{p,t-1} \phi_{p,t-1}^j + \phi_{p,t-1}^{Ad} + \omega_{p,t-1}$$

and the total population growth rate of each plot across all four years was measured as the geometric mean of the annual rates (Pulliam 1996):

$$\lambda_p = \left[ \prod_{t=1}^3 \lambda_{p,t} \right]^{1/3}$$

The above equations represent the total contribution of all three classes of individuals (local recruits, surviving adults, and immigrants) to local population growth. In some cases, populations that cannot support themselves through local recruitment processes may experience positive populations growth ( $\lambda > 1$ ) due to high immigration rates. To measure the ability of each plot to maintain itself through retention and self-recruitment only, known as the self-recruitment rate ( $R_p$ , Runge et al. 2006), we also calculated:

$$R_{p,t} = f_{p,t-1} \phi_{p,t-1}^j + \phi_{p,t-1}^{Ad}$$

Note that  $R_p$  cannot be calculated from either point count or MAPS data because it is not possible to know which captured or recorded individuals were born on the plot itself, and which immigrated there. We examined the correlation among population growth estimates using simple Pearson correlation coefficients.

### Local and Landscape Predictors of Population Growth

To examine the predictors of population growth we built competing models with self-recruitment rate ( $R$ ) as our response variable and various combinations of local and landscape variables as predictors. We specifically chose self-recruitment as our response variable because it

measures the key local recruitment processes that contribute to stable population size. Moreover, sites that have self-recruitment rate  $> 1$  are important to regional population dynamics as they make measureable contributions to the focal subpopulation (Donacaster et al. 1997). We used two structural elements of local vegetation (shrub cover and the number of trees with DBH greater than 30), as well as two landscape variables (patch size and amount of forest cover within 2 km) as fixed effects and plot as a random effect. We used only a subset of local vegetation characteristics because of collinearity among predictors and because previous work suggested that both shrub cover and stand age were important habitat selection features for Wood Thrush (Evans et al. 2011). We assessed model suitability by comparing Akaike's information criterion values corrected for small sample sizes ( $AIC_c$ ), and model weights ( $w_i$ ). We iteratively dropped fixed effects and compared models to a null model with only random effects. Those models with  $\leq 2 \Delta AIC_c$  were considered equally supported (Burnham and Anderson 2002; Bolker et al. 2009). Because the response and predictor variables were on vastly different scales (e.g., R: 0-1; Count of trees: 492-5146) we log transformed response variables to make beta coefficients interpretable. Data were analyzed using the lmer function from the lme4 (Bates et al. 2014) and bbmle (Bolker et al. 2014) packages available in the statistical program R version 3.0.2 (R Core Team 2013).

## Results and Discussion

### Comparing Population Growth Estimates

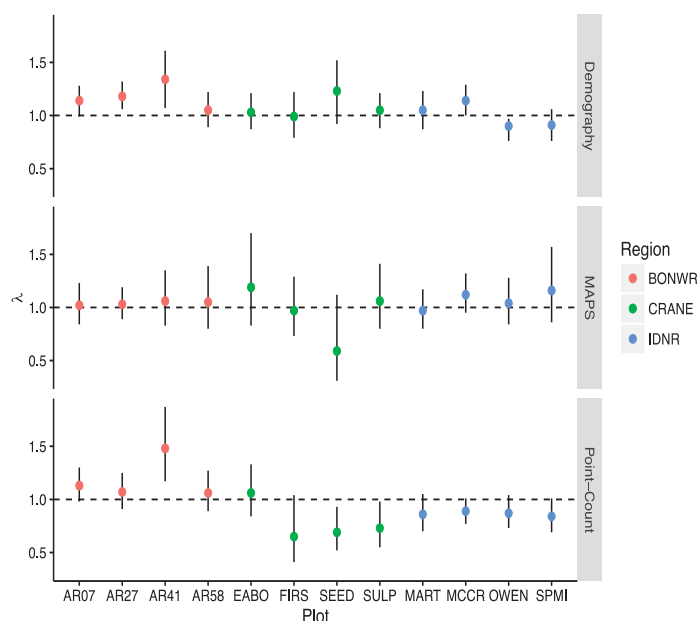
Estimates of population growth showed the strongest concordance among study sites at the Big Oaks National Wildlife Refuge, all of which were categorized as sources ( $\lambda > 1$ ) using all three methods (Table 4.1; Fig. 4.1). In contrast, Indiana Department of Natural Resource sites which are variable sized forest fragments and Crane sites and are managed via selective harvest, showed substantially less agreement in source vs. sink designation. These results suggest that sources may be intrinsically easier to identify using methodologically diverse techniques. This is likely because high-quality source habitats are demographically stable through time with less variance in the key vital rates that contribute to population growth (see Chapter 3). In contrast, low-quality sink habitats have smaller overall population sizes and therefore are more likely to experience significantly more demographic stochasticity causing temporal switches between source and sink. Higher variance in  $\lambda$  would be harder to quantify with techniques that do not account for all vital rates that can drive population dynamics. Here, we have presented cumulative estimates of  $\lambda$  which undoubtedly tell us about a population trend through time. Temporal variation in demography may be a relevant factor depending upon the management scheme. Although MAPS and point-count estimates of population growth can't recover these long-term trends, they perform better when looking at finer temporal scale estimates population change (see future directions).

**Table 4.1** Population growth estimates derived from methodologically diverse avian sampling techniques. Data was collected from 2011 to 2014 at two DoD installations (Big Oaks National Wildlife Refuge, BONWR and Crane Naval Facility, CRANE) and at surrounding properties managed by Indiana Department of Natural Resources. Plots represent a gradient in habitat quality as well as variation in patch size and regional forest connectivity.

Region	Plot	$\lambda_{PC}$	$\lambda_{MAPS}$	$\lambda_{ID}$	$R$
BONWR	AR27	1.07	1.03	1.18	1.22
BONWR	AR41	1.48	1.06	1.34	1.09
BONWR	AR07	1.13	1.02	1.14	1.02

BONWR	AR58	1.06	1.05	1.05	0.94
IDNR	MCCR	0.89	1.12	1.14	1.07
IDNR	MART	0.86	0.97	1.05	0.89
IDNR	OWEN	0.87	1.04	0.9	0.77
IDNR	SPMI	0.84	1.16	0.91	0.88
CRANE	EABO	1.06	1.19	1.03	0.75
CRANE	FIRS	0.65	0.97	0.99	0.62
CRANE	SEED	0.69	0.59	1.23	0.6
CRANE	SULP	0.73	1.06	1.05	0.9

In examining the concordance among estimates of lambda derived from each approach, we found substantial evidence for a moderately strong correlation between  $\lambda_{PC}$  and  $\lambda_{ID}$  (Pearson's  $r = 0.54$ ,  $t = 2.07$ ,  $df = 10$ ,  $p = 0.06$ ). In contrast, we found little evidence for significant correlation between estimates derived from MAPS data and the other two approaches ( $\lambda_{MAPS}$ - $\lambda_{ID}$ ,  $r = -0.37$ ,  $t = -1.26$ ,  $df = 10$ ,  $p = 0.24$ ;  $\lambda_{MAPS}$ - $\lambda_{PC}$ ,  $r = 0.37$ ,  $t = 1.27$ ,  $df = 10$ ,  $p = 0.23$ ). Despite the weak correlation point-counts and intensive demography data often differently categorized plots as sources and/or sinks which could create a problem for population monitoring and management. Failure to find strong concordance among these approaches could result from differences in the sensitivity of each approach to detect key changes in demographic vital rates and/ or these methods may measure processes from different spatial scales.



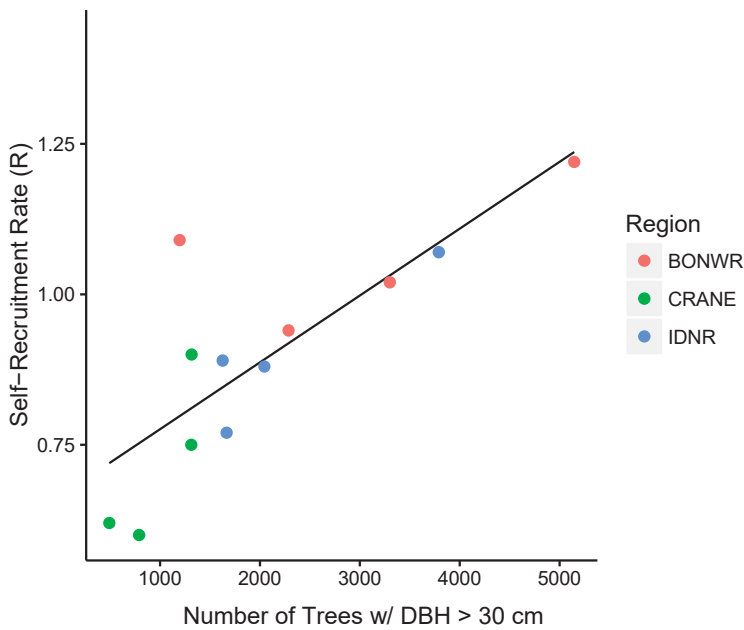
**Figure 4.1** A comparison of population growth estimates (points) and 95% confidence intervals (error bars) for point-count, MAPS and demographic

Understanding the spatial scale from which demographic data are sourced is key to interpreting the similarities and differences between  $\lambda$  estimates produced by the various sampling approaches. The intensive demographic estimates are generated as a function of locally estimated fecundity, recruitment, adult survival, and immigration rates. Moreover, this is the first demographic model that has incorporated vital rates across the annual cycle. The error contained in each of these demographic estimates is jointly propagated to the  $\lambda$  estimate using the Bayesian integrated population modeling framework. Nonetheless, all estimates are generated from nests and individuals that are known to have originated in

the plot of interest, making these estimates the most reliable information obtainable about local growth rates. To our knowledge, this is the most comprehensive and data rich avian population model ever built making it as close to demographic truth as current avian sampling and analytical methods can approximate. On the other hand, both MAPS and point count data utilize capture-recapture histories and/or count data to generate growth estimates. While the former approach contains more detailed information in the form of uniquely identified individuals, both suffer from

a scaling issue; that is, it is unclear what spatial area is being sampled by MAPS and point count data.

For instance, MAPS data rely on a ratio of adults to juveniles to produce productivity estimates (see Chapter 2), but there is no guarantee that an adult individual captured in a given mist net is locally territorial, or that a captured juvenile was locally recruited. Floating birds (Penteriani et al. 2011) can frequently make up large portions of an adult population, and often do not have any home range, per se, such that the location in which they are captured may be random with respect to their origin or where they eventually breed. In addition, mean post-fledging dispersal distances for Wood Thrush range from 1.5 km in Virginia (Vega Rivera et al. 1998) to 2.08 km in Missouri (Anders et al. 1998), and may be as large as 5.3 km. Because juvenile Wood Thrush fledged as early as the first week of June in our study region, the original capture locations for many young birds may more accurately reflect dispersal territory preferences, rather than local productivity. Finally, independent juveniles disperse to habitats with dense understories (e.g., early to mid-successional or riparian forests) that provide both abundant food and protection from predators (Anders et al. 1998, Fink 2003). These differences in habitat preference between dispersing juveniles and adults could produce misleading ratios as young birds move out of natal source habitats with a large number of breeders and into habitats that are dominated by early successional vegetation with far fewer breeding adults. As a result,  $\lambda$  estimates stemming from the MAPS protocol may represent information from a much broader spatial area than what was actually sampled.



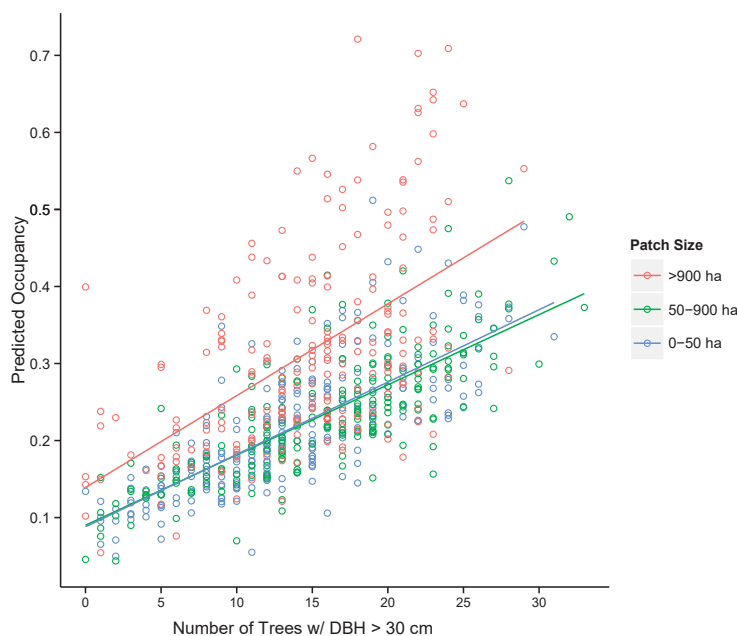
**Figure 4.2.** The number of large trees was the best predictor of Wood thrush demographic performance in southern Indiana from 2011 to 2104. Points represent demographic performance of the 12 study populations and the line is the model prediction from our GLMM ( $\beta_{\text{BAG30}} = 0.21 \pm 0.05$ ). Large trees were also a good proxy for other key habitat variables including understory shrub density, vertical structure and leaf litter depth all of which are important for Wood thrush performance.

The  $\lambda$  estimates from the point count data are based on even coarser information than that used in the MAPS approach. Here, population growth rates roughly represent a simple ratio of site abundance in year  $t$  to site abundance in year  $t-1$ . While a “site” was defined as a 50 m radius circle, this approach still suffers from the fact that floater adults could be detected during a point count even though they do not regularly utilize that space. Further, as demonstrated in Chapter 1, territories of individuals may frequently only partly overlap the sampling space, making estimation of the actual area sampled impossible (Nichols et al. 2009). On the other hand, juvenile birds are very rarely detected during point count surveys due to their cryptic nature, and thus  $\lambda_{\text{PC}}$  estimates are

likely free of any biases stemming from dispersing hatch-year birds. In fact, greater than 80% of



our Wood Thrush detections during point count sampling were of singing adult males. Given that  $\lambda_{ID}$  estimates were generated from a female-only population model, at the correspondence between  $\lambda_{ID}$  and  $\lambda_{PC}$  estimates (Table 4.1; Fig. 4.1) is surprising, but potentially important. We suspect these results indicate that point counts are relatively good indicators of local abundance, and changes in local abundance, even if density cannot be accurately calculated. That is, even though the effective area sampled by a single point count cannot be accurately estimated (unless repeated samples are conducted extremely close in time; see Chapter 1), the variability in sample area would be on par with the range in territory dimensions (0.08 – 4 ha for Wood Thrush; Evans et al. 2011). In other words, the effective radius of our point counts was likely somewhere between 50 and 250 m (though validation of this educated guess is left to future work). Therefore, the extent of most of our point count samples were likely contained completely within the boundaries of the plots outlined for demographic sampling, and effectively represented the same area.



**Figure 4.3.** A plot of predicted Wood Thrush occupancy at the point count station scale as a function of the number of trees with DBH > 30 cm.

patch size and/ or forest cover within 2 km. The lack of support for models with landscape scale variables indicates that managers may be able to provide high productivity Wood Thrush habitat using simple fine scale manipulations. Simply encouraging growth and retention of large trees will create sites that are both high quality (Fig. 4.2). These management practices might also require minimizing selective timber harvest which impacts both overstory and understory forest structure. In addition to having a positive demographic impact, management practices that encourage retention of large trees will also be preferentially selected by Wood thrush (Fig. 4.3) thereby increasing overall occupancy. Increasing regional occupancy will undoubtedly buffer and increase the likelihood of persistence for local and regional populations.

Although these models of local productivity underscore the importance of large trees, and more broadly local vegetation structure, we do not feel our results rule out the importance of landscape scale features. Other results presented here in this report show that regional processes,

### Local and Landscape Predictors of Population Growth

The only model of self-recruitment rate that had substantial support (i.e.,  $\Delta AIC < 2$ ; Burnham & Anderson 2002) contained a single explanatory variable, number of trees with DBH > 30 cm. Importantly, many of the local scale habitat features are collinear such that habitats with a high number of large trees are also characterized by high shrub density, complex vertical structure (i.e., sub-canopy) and high leaf litter depth (see Table 1.4) all of which are likely important for Wood thrush habitat selection as well as productivity. In contrast, we found little to no support for landscape level variables such as



specifically immigration, can play an essential role in converting sink habitats into sources. The MAPS results show that region forest cover with 2km was a significant predictor of local productivity. As discussed above MAPS reproductive index may measure larger spatial scale productivity and these processes may buffer populations. Moreover, the results from our integrated population model show clearly that immigration processes are important across a gradient of habitat quality. Ultimately, our results show clearly that local land management can have a positive demographic impact, yet land managers must consider regional land use especially when considering the rescue of populations in demographic deficit.

**Table 4.2.** A comparison of models developed to test the effects of local and landscape level variables on self-recruitment rate. Local variables considered in model development were number of trees with DBH greater than 30 cm (BAG30) and shrub cover (SC), while landscape variables included patch size (Patch) and amount of forest cover within 2 km.

Model	$\Delta AICc$	logLik	$w_i$
<i>BAG30</i>	0.0	4.0	0.66
<i>Null</i>	2.3	1.9	0.21
<i>BAG30+ForCov+Patch</i>	5.0	3.5	0.06
<i>BAG30+Patch</i>	6.2	1.9	0.03
<i>SC+BAG30+ForCov+Patch</i>	7.0	3.5	0.02
<i>Patch</i>	8.0	0.0	0.01
<i>ForCov+Patch</i>	9.0	0.5	0.00

## Conclusions and Implications for Future Research

Our results definitively show that the point count and intensive demographic approaches we demonstrated provide very similar estimates of  $\lambda$ . The MAPS protocol, on the other hand, produced estimates that were not significantly, and in some cases not positively, correlated with either the point count or demographic estimates. As mentioned, we hypothesize that these results are indicative of similarities in spatial areas sampled by point counts and demographic monitoring, while the MAPS protocol samples an area that is geographically much larger. Validation of this hypothesis is beyond the scope of this study, but future work should investigate the source of this discrepancy. Further, despite the correlation between point count and demographic  $\lambda$  estimates, in 4 of 12 cases point counts identified sites as having a negative population trajectory when the “true” estimates from demographic monitoring indicated positive growth. Point count methodology may thus be less useful as a classification tool than it is for ranking population trajectories of multiple sites relative to one another. In addition, our results technically only apply to a single species in a single geographic region, and future studies should investigate whether point counts can be used universally as a reasonable substitute for demographic monitoring. For instance, we may not expect to find similar correspondence between point count and demographic estimates of  $\lambda$  for species with larger home ranges, or more cryptic vocalization tendencies.

Ultimately,  $R_p$ , the self-recruitment rate, is probably the most reliable indicator of whether a site could be considered a source or a sink. The  $\lambda$  estimates generated by any of the three approaches we took are heavily influenced by immigration rate, and thus  $\lambda$  estimates could be positive even if the site is incapable of sustaining itself. Ecologists have long recognized that density, or changes in density are not necessarily indicative of habitat quality (Van Horne 1983), and in this respect, there is no substitute for intensive demographic monitoring if local population

management is the goal. If, however, interest is simply in spatial variation in population growth rate, repeated point count sampling over multiple years may provide reasonable approximations at substantially reduced cost, and over much broader spatial scales. As mentioned above, future research will investigate if temporally refined estimates of  $\lambda$  produced from point-count data more reliably recover the demographic performance of a population. Finally, it is important to highlight that both lower unit cost effort and data resolution approaches (count and MAPS) do a good job of categorizing source populations in high quality habitats.

Our results indicate that encouraging Wood Thrush population growth is merely a matter of growing and maintaining large trees. Fortunately, the factors that attract breeding Wood Thrush are the same as those that result in positive population growth, eliminating concern about ecological traps (e.g., Kristan 2003). These results are emphasized by the fact that the BONWR sites in our study that had both the greatest population growth, and the least amount of local vegetation management. Sites where selective harvesting of large trees was common (e.g., Crane plots) tended to have low or negative population growth. This commentary is not intended as a criticism of the forest management practices on Crane, but rather as a simple statement of fact about how they likely impact local Wood Thrush populations. We recognize that selective harvesting is almost certain to benefit other avian and mammalian species, even if it does not directly benefit Wood Thrush. It should also be noted that while the count of large trees is the single greatest predictor of self-recruitment rate, this does not mean that landscape features have no influence on Wood Thrush population persistence. Technically, a self-sustaining site may not be a source at all if surplus individuals are not able to disperse to and colonize other habitat patches (Pulliam 1988). In this sense, while landscape configuration may have little influence on local growth rate, it may have substantial influence on connectivity of high and low quality areas. Understanding how landscape configuration influences bird dispersal and mobility was beyond the scope of this project. We have, however, recently begun a series of translocation experiments on Crane and surrounding areas to investigate how landscape features influence the permeability of the landscape for Wood Thrush and other species. To date, no studies have parameterized predictive models of population persistence with real demographic data to provide guidance on optimal management strategies (Lloyd et al. 2005). In the future, we intend to combine our newly gathered dispersal information with the data gathered in this report to produce a realistic individual-based computer model that will allow us to categorize source-sink dynamics at regional scales and make predictions about how the ratio of sources and sinks in the landscape determines population viability.

In this report, we have provided a wealth of information about Wood thrush population dynamics, yet management decisions often need to be made based on competing demands and must take into consideration multiple taxonomic groups. Although managing suites of species can be difficult, we believe our results provide some key insight into the ecological processes that influence the distribution and population dynamics for birds on DoD installations in Southern Indiana and more broadly across the eastern deciduous forest region. In Chapter 1 and here in Chapter 4 we have shown that point-counts and occupancy modeling are a useful tool for characterizing patterns of avian spatial distribution and monitoring stable populations. Point counts can also provide information about the whole community of birds on DoD installations and therefore increase the ability of managers to make management decisions that maximize biodiversity. Examining the predictors of occupancy from Chapter 1 shows that species respond to different aspects of local habitat and landscape configuration. For example, occupancy of edge species is maximized when forest patches are small and have sufficient successional edge habitat

available for breeding. In contrast, the occupancy of forest interior species is maximized by increasing patch size, but not necessarily overall forest cover. As such, maximizing avian diversity on installations will require managers to maintain a heterogeneous configuration of patch sizes as well as compositional makeup. Importantly, our results also suggest that landscape features largely act as a coarse-scale filter that determines the presence-absence of species and to some extent their abundance. Although count data are less precise when it comes to understanding species-specific demography, they can be used as a heuristic tool when both occupancy and demographic data are available for a single species. Below we outline how patterns of occupancy and temporal changes in abundance can inform population dynamics for species with similar habitat requirements.

Interior forest specialist species have shown among the most dramatic population declines over the last decade and as a result are ranked as the highest conservation concern (NABCI 2016). In particular, Wood thrush, Kentucky warbler and Acadian flycatcher are all interior forest specialists that have significantly negative trends (-1.13, -0.92, -0.45, respectively) in the central hardwood region based on long-term Breeding Bird Survey count data. As such, all three are recognized as species of concern by DoD. Our results suggest these three species, as well as most others grouped within the interior community, require large forest patches. Moreover, the occupancy results also show that these species respond to fine scale habitat features (Table 1.13) whereby occupancy increases in habitats with large trees, high shrub cover and vertical foliage density. In Chapter 3 and 4 we found that key Wood thrush demographic vital rates and self-recruitment were influenced by fine-scale habitat variables (Fig. 3.4 & Table 4.2). Congruence between the occupancy results and the key drivers of self-recruitment rate for Wood thrush suggest that count data can potentially be an accurate indicator of demographic performance for a broader suite of interior forest birds. These patterns further suggest that Wood thrush is a good umbrella species upon which to make management decisions for this group of species that is of conservation concern. Although, we do not have detailed demographic for all species, MAPS monitoring provides us with apparent breeding season survival, which is one of the top three contributors to variance in population growth (see Chapter 3). Future work with MAPS data will investigate the key predictors of survival across suites of species and then look for congruence with the drivers of occupancy. This approach may be able to find suites of species that would benefit from similar management strategies like the interior species highlighted above. Ultimately management decisions will be both scale and objective dependent. Our occupancy data highlight how installations can maximize avian diversity through landscape composition and configuration and our demographic data suggest how fine scale habitat can be managed to ensure population persistence. These strategies may not be mutually exclusive, but the complexity and diversity of species of breeding birds monitored suggested that no single catch-all management solution is likely to exist. As an addendum to our report we are providing DoD land managers with a user's guide to begin thinking strategically about how to structure monitoring programs to meet specific management objectives.

### Literature Cited

- Allredge, M.W., Pollock, K.H., Simons, T.R., Collazo, J.A. & Shriner, S.A. (2007) Time-of-detection method for estimating abundance from point-count surveys. *The Auk*, **124**, 653–664.
- Anders, A.D., Faaborg, J. & Thompson III, F.R. (1998) Postfledging dispersal, habitat use, and home-range size of juvenile Wood Thrushes. *The Auk*, **115**, 349–358.
- Bart J., Manning A., Dunn L., Fischer R. & Eberly C. (2010) A coordinated bird-monitoring plan for the Department of Defense. Report prepared for the Department of Defense Legacy

- Resource Management Program.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. (2014) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6.
- Betts, M.G., Rodenhouse, N.L., Sillett, T.S., Doran, P.J. & Holmes, R.T. (2008) Dynamic occupancy models reveal within-breeding season movement up a habitat quality gradient by a migratory songbird. *Ecography*, **31**, 592–600.
- Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. S. White. (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution*, **24**, 127-135.
- Bolker, B. and R Development Core Team. (2014) bbmle: Tools for general maximum likelihood estimation. R package version 1.0.17.
- Breining D.R., Larson V.L., Duncan B.W., Smith R.A., Oddy D.M. & Goodchild M.F. (1995) Landscape patterns of Florida scrub jay habitat use and demographic success. *Conservation Biology* **9**, 1442–1453.
- Burnham, K., and D. Anderson. 2002. Model selection and multi-model inference: a practical information theoretic approach. 2nd edition. Springer-Verlag, New York, New York, USA.
- Dail, D. & Madsen, L. (2011) Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, **67**, 577–587.
- DeSante D.F. (1990) The role of recruitment in the dynamics of a Sierran subalpine bird community. *American Naturalist*, **136**, 429-455.
- DeSante, D.F. (1995) Suggestions for future directions for studies of marked migratory landbirds from the perspective of a practitioner in population management and conservation. *The Journal of Applied Statistics*, **22**, 949-965.
- Doncaster C.P., Clobert J., Doligez B., Gustafsson L. & Danchin E. (1997) Balanced dispersal between two spatially varying local populations: an alternative to the source-sink model. *American Naturalist*, **150**, 425-444.
- Donovan T.M., Thompson F.R., Faaborg J. & Probst J.R. (1995) Reproductive success of migratory birds in habitat sources and sinks. *Conservation Biology*, **9**, 1380-1395.
- Evans, M., Gow, E., Roth, R.R., Johnson, M.S., & Underwood, T.J. (2011) Wood Thrush (*Hylocichla mustelina*). The Birds of North America (P.G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, NY.
- Fauth PT. (2001) Wood thrush populations are not all sinks in the agricultural Midwestern United States. *Conservation Biology*, **15**, 523–527.
- Fink, M. L. (2003) Post-fledgling Ecology of Juvenile Wood Thrush in Fragmented and Contiguous Landscapes. Ph.D. dissertation, University of Missouri-Columbia, Columbia, MO, United States of America.
- Flather CH and Sauer JR. (1996) Using landscape ecology to test hypotheses about large-scale abundance patterns in migratory birds. *Ecology*, **77**, 28-35
- George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. (1992) Impacts of a severe drought on grassland birds in western North Dakota. *Ecol. Appl.*, **2**, 275-284
- Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.
- Hatchwell BJ, Chamberlain DE and Perrins CM. (1996) The demography of blackbirds *Turdus merula* in rural habitats: is farmland a sub-optimal habitat? *Journal of Applied Ecology*, **33**, 1114–1124.

- Hoover JP, Brittingham MC and Goodrich LJ. (1995) Effects of forest patch size on nesting success of wood thrushes. *Auk*, **112**, 146-155.
- James FC, McCulloch CE and Wiedenfeld DA. (1996) New approaches to the analysis of population trends in land birds. *Ecology*, **77**, 13-27.
- Kendall, W. L., and J. D. Nichols. (2002) Estimating state- transition probabilities for unobservable states using cap- ture–recapture/resighting data. *Ecology*, **83**, 3276–3284.
- Kendall, W. L., and J. D. Nichols. 2004. On the estimation of dispersal and movement of birds. *Condor*, **106**, 720–731.
- Kery M and Royle JA. (2010) Hierarchical modelling and estimation of abundance and population trends in metapopulation designs. *Journal of Animal Ecology*, **79**, 453-461.
- Kristan, W.B. (2003) The role of habitat selection behavior in population dynamics: source-sink systems and ecological traps. *Oikos*, **103**, 457–468.
- Laake, J. L. (2013) RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01. Seattle, WA.
- Larson MA, Thompson FR, Millspaugh JJ, Dijak WD and Shifley SR. (2004) Linking population viability, habitat suitability, and landscape simulation models for conservation planning. *Ecological Modelling*, **180**, 47-58
- Lloyd P, Martin TE, Redmond RL, Langner U and Hart MM. (2005) Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications*, **15**, 1504-1514.
- Lloyd-Evans TL and Atwood JL. (2004) 32 years of changes in passerine numbers during spring and fall migrations in coastal Massachusetts. *Wilson Bulletin*, **116**, 1-16.
- Mumme RL, Schoech SJ, Woolfenden GE and Fitzpatrick JW. (2000) Life and death in the fast lane: demographic consequences of road mortality in the Florida scrub-jay. *Conservation Biology*, **14**, 501–512.
- Nichols, J.D., Thomas, L. & Conn, P.B. (2009) Inferences about landbird abundance from count data: recent advances and future directions. *Modeling Demographic Processes in Marked Populations* (eds D.L. Thomson, E.G. Cooch & M.J. Conroy), pp. 201–235. Springer Science+Business Media, LLC, New York.
- Noon, B. R. and J. R. Sauer. (1992) Population models for passerine birds: structure, parameterization, and analysis. (eds D. R. McCullough and R. H. Barrett), pp. 441-464 *Wildlife 2001: Populations*. Elsevier Applied Science, New York, New York.
- Nott MP and Morris T. (2007) Performance Measure Analysis: Examples of comparing and contrasting installation-specific demographics with regional demographics and landscape characteristics. (Tech. report to the U.S. Department of Defense Legacy Resources Management Program, Contribution No.324 of The Institute for Bird Populations, Point Reyes Station, CA.).
- Penteriani, V., Ferrer, M. & Delgado, M.M. (2011). Floater strategies and dynamics in birds, and their importance in conservation biology: towards an understanding of nonbreeders in avian populations. *Anim. Conserv.*, **14**, 233–241.
- Pradel R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. *Biometric*, **52**, 703-709.
- Pulliam, H.R. (1988) Sources, Sinks, and Population Regulation. *Am. Nat.*, **132**, 652–661.
- Pulliam, H.R. (1996) Sources and Sinks: Empirical evidence and population consequences. In: *Population Dynamics in Ecological Space and Time* (eds. Rhodes, O.E., Chesser, R.K. & Smith, M.H.). University of Chicago Press, Chicago, IL, pp. 45–69.



- Pulliam HR and Danielson BJ. (1991) Sources, Sinks, and Habitat Selection: A Landscape Perspective on Population Dynamics. *American Naturalist*, **137**, S50.
- Robbins CS, Sauer JR, Greenberg RS and Droege S. (1989) Population declines in North American birds that migrate to the Neotropics. *PNAS*, **86**, 7658-7662.
- Robinson SK, Thompson FR, Donovan TM, Whitehead DR and Faaborg J. (1995) Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987-1990.
- Rota, C.T., Fletcher Jr, R.J., Dorazio, R.M. & Betts, M.G. (2009) Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, **46**, 1173–1181.
- Runge, J.P., Runge, M.C., Nichols, J.D., Stamps, A.E.J.A. & DeAngelis, E.D.L. (2006). The Role of Local Populations within a Landscape Context: Defining and Classifying Sources and Sinks. *Am. Nat.*, **167**, 925–938.
- Saracco, J. F., D. F. Desante, and D. R. Kaschube. (2008) Assessing Landbird Monitoring Programs and Demographic Causes of Population Trends. *Journal of Wildlife Management*, **72**, 1665–1673.
- Sauer, J. R., G. W. Pendleton, and B. G. Peterjohn. (1996) Evaluating causes of population change in North American insectivorous songbirds. *Conservation Biology* **10**, 465-478.
- Sauer JR and Link WA. (2002) Hierarchical modeling of population stability and species group attributes from survey data. *Ecology*, **83**, 1743-1751.
- Sherry, T. W. and R. T. Holmes. (1995) Summer versus winter limitation of populations: What are the issues and what is the evidence. Pages 85-120 in *Ecology and management of Neotropical migratory birds: A synthesis and review of critical issues*. (T. E. Martin and D. M. Finch, eds.) Oxford University Press, New York.
- Sillett, T.S. & Holmes, R.T. (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. *J. Anim. Ecol.*, **71**, 296–308.
- Van Horne B. (1983) Density as a Misleading Indicator of Habitat Quality. *Journal of Wildlife Management*, **47**, 893-901.
- Vega Rivera, J.H., Rappole, J.H., McShea, W.J. & Haas, C.A. (1998) Wood Thrush postfledging movements and habitat use in northern Virginia. *The Condor*, **100**, 69–78.
- Vierling KT. (2000) Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. *Ecological Applications*, **10**, 1211–1218.
- Villard MA, Trzcinski MK and Merriam G. (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conservation Biology*, **13**, 774-783.
- Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT. (2002) Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution*, **17**, 76-83.
- White, G., and K. Burnham. (1999) Program MARK : survival estimation from populations of marked animals. *Bird Study*, **46**, 120–138.
- Zhou S and Griffiths SP. (2007) Estimating abundance from detection-nondetection data for randomly distributed or aggregative elusive populations. *Ecography*, **30**, 537-549.